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CONTENTS

Vertical Distribution of the Plankton Rotifera in Douglas Lake,
Michigan, with Special Reference to Depression Individuality

ROBERT S. CAMPBELL

(Pp. 1-19)

Limnological Studies in Connecticut, IV. Mechanism of
Intermediary Metabolism in Stratified Lakes

G. EVELYN HUTCHINSON

(Pp. 21-60)

The Vegetation of Roan Mountain: A Phytosociological
and Successional Study

D. M. BROWN

(Pp. 61-97)

An Oceanographic Consideration of the Dinoflagellate
Genus *Ceratium*

HERBERT W. GRAHAM

(Pp. 99-116)

Vegetation on the Peat Lands of Dane County, Wisconsin

A. L. FROLIK

(Pp. 117-140)

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VERTICAL DISTRIBUTION OF THE PLANKTON ROTIFERA
IN DOUGLAS LAKE, MICHIGAN,
WITH SPECIAL REFERENCE TO SUBMERGED
DEPRESSION INDIVIDUALITY*

ROBERT S. CAMPBELL

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* Contribution from the Biological Station and from the Department of Zoology, University of Michigan.

TABLE OF CONTENTS

	PAGE
INTRODUCTION	3
METHODS	3
HYDROGRAPHY	3
ANNOTATED LIST OF PLANKTON ROTIFERA FROM DOUGLAS LAKE	4
THERMO-CHEMICAL DEPRESSION INDIVIDUALITY	5
Thermal Conditions	5
Stratification	5
Bottom-water Temperatures	7
Chemical Conditions	10
Dissolved Oxygen	10
Free Carbon Dioxide	11
Hydrogen-ion Concentration	11
Alkalinity	11
Winter Records	12
DEPRESSION INDIVIDUALITY WITH RESPECT TO VERTICAL DISTRIBUTION OF THE ROTIFERA	12
Evidence from Population Totals	12
Evidence from Species	13
SEASONAL VARIATION IN VERTICAL DISTRIBUTION	13
Distribution of Total Rotifera	13
Species Distribution	15
SEASONAL CHANGES IN ABUNDANCE	16
SUMMARY	18
LITERATURE CITED	18

VERTICAL DISTRIBUTION OF THE PLANKTON ROTIFERA IN DOUGLAS LAKE, MICHIGAN, WITH SPECIAL REFERENCE TO SUBMERGED DEPRESSION INDIVIDUALITY

INTRODUCTION

Douglas Lake, Michigan, is especially favorable for the study of submerged depression individuality. The main basin contains seven distinct submerged depressions separated by relatively shallow water. An examination of their physical and chemical conditions has shown that they behave as if they were seven separate lakes, varying markedly in sharpness and extent of both thermal and chemical stratification. This depression individuality has been discussed in detail by Welch (1927) and by Welch and Eggleton (1932, 1935). From time to time evidences of a corresponding biological individuality have been observed. Yoshimura (1931) reported differences in the distribution of *Corethra* larvae among the submerged basins of Lake Akimoto, Japan. Scott, Hile and Spieth (1938) found quantitative differences in *Corethra* and Chironomidae among three submerged basins in Tippecanoe Lake, Indiana. Depression individuality in terms of qualitative differences of bottom fauna was demonstrated for Douglas Lake by Eggleton (1931). Scott (1931) presented comparative plankton counts for several of the numerous secondary basins within James Lake, Indiana, which indicated both qualitative and quantitative differences.

This investigation dealt with a comparison of the vertical distribution and abundance of the plankton Rotifera in the seven submerged depressions of Douglas Lake, and the relation of these data to the known chemical and physical differences among depressions. It is based upon 641 plankton samples of which 574 were taken at approximately monthly intervals throughout 1937, and at 2-week intervals throughout 1938, exclusive of the periods of ice cover. The 1933-34 winter data are based upon 67 samples from plankton collections loaned by Drs. David C. Chandler and Donald E. Miller.

The writer wishes to express his indebtedness to Professor Paul S. Welch under whose direction this work was done; to Mr. Frank J. Myers for the identification of collections of rotifers submitted to him; and to Drs. David C. Chandler and Donald E. Miller for the use of winter plankton collections and winter thermo-chemical data from Douglas Lake.

METHODS

A Negretti and Zambra reversing thermometer was used for all temperature records. Water samples both for chemical analyses and for plankton content were collected with a modified Kemmerer sampler. Precautions were taken to insure that all samples were strictly comparable. Procedures outlined in the 1936 edition of Standard Methods for the Examination of Water and Sewage have been followed in the determination of dissolved oxygen, free carbon dioxide and

alkalinity. Hydrogen-ion concentration was measured colorimetrically by comparison with La Motte color standards.

Thermal and chemical determinations were made prior to every plankton collection, the procedures for oxygen analysis being completed in the field to the point of liberation of free iodine. Thus absence of oxygen from any sample was immediately discernible and the distribution of plankton samples governed accordingly. In regions of abrupt thermal and chemical change, samples have been spaced at one-meter intervals, since such regions usually showed abrupt population changes. Ten samples with a Kemmerer sampler were made at each depth investigated. Since the different samplers varied in capacity, the precise amounts delivered by each were always carefully measured. But for purposes of a general statement here, the total volume of 10 such samples amounted to approximately 12.5 liters. The water so obtained was delivered into a No. 25 silk bolting-cloth plankton net suspended in the neck of a 5-gallon milk can. Formaldehyde was added immediately to the concentrate in sufficient amounts to insure preservation.

Whether 10 closely-spaced samples will give a correct measure of the total rotifer population of the depression at that depth depends chiefly upon the character of the horizontal rotifer distribution. A similar circumstance is discussed in some detail for the limnetic Crustacea of Lake Nipissing by Langford (1938). Since the completion of any one of the series including the seven depressions required approximately three days, it was not possible to determine, prior to every sampling date, the nature of the horizontal plankton distribution within each depression. Therefore, only pronounced concentration differences among depression populations or consistent dissimilarities among depression populations where the numbers of individuals involved were small are considered in this paper. Collections were usually completed between the hours of 6:00 A.M. and 6:00 P.M.

Following the work of Raymond (1937), all rotifers in two 1.25 cc. samples from every concentrate were counted and the counts converted into the number of individuals per liter of lake water.

HYDROGRAPHY

Morphometric data concerning Douglas Lake have been presented by Welch (1927). The seven depressions, together with their isolation contours and maximum depths, are shown on the accompanying map (Fig. 1). Of the seven depressions, South Fish-Tail alone has a certain protection from the prevailing northwest winds. This partial protection is provided by an elevated promontory.

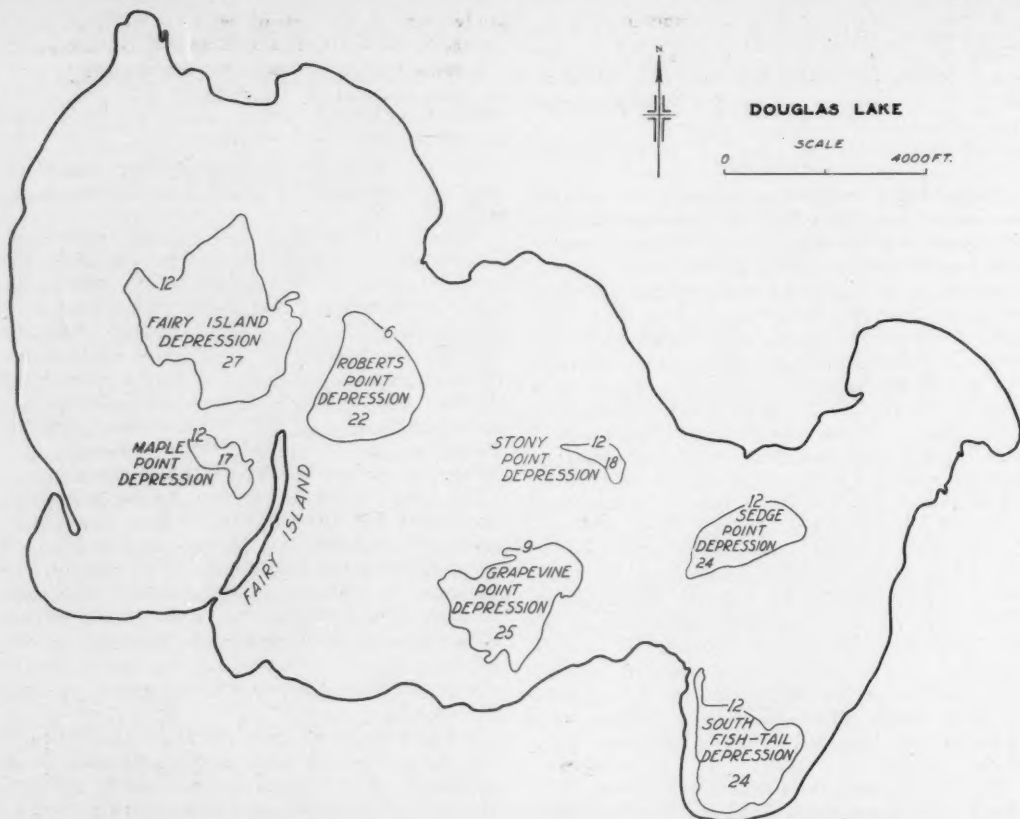


FIG. 1. Map of Douglas Lake, Michigan, indicating positions of seven submerged depressions. Isolation contours are shown for each depression. The figure on each contour indicates its depth in meters. Maximum depths in meters are expressed by the numerals within the depression contours. Map redrawn, with slight modification, from Welch (1927).

ANNOTATED LIST OF PLANKTON ROTIFERA FROM DOUGLAS LAKE

- Ascomorpha ecaudis* Perty
Asplanchna priodonta Gosse
Collotheca mutabilis (Hudson)
Conochilus unicornis Rousselet
Filinia longiseta (Ehrenberg)
Gastropus stylifer Imhof
Kellicottia bostoniensis (Rousselet)
Kellicottia longispina (Kellicott)
Keratella cochlearis (Gosse)
Keratella cochlearis f. *longispina* Imhof. This form was not separated in counting but is included under *Keratella cochlearis* (Gosse).
Keratella cochlearis f. *macracantha* (Lauterborn)
Keratella cochlearis f. *robusta* (Lauterborn)
Keratella quadrata var. *brevispina* (Gosse)
Keratella quadrata var. *divergens* (Voigt). Individuals from Douglas Lake are characterized by stout posterior spines which have a peculiar sigmoidal curve. Mr. Myers concluded that this is a form of *Keratella quadrata* var. *divergens* (Voigt).

Notholca striata (Müller)

Ploesoma spp. Including both *Ploesoma lenticulare* (Herrick) and *Ploesoma truncatum* (Levander), which were not separated in counting.

Polyarthra euryptera Wierzejski

Polyarthra trigla Ehrenberg

Pompholyx complanata Gosse

Trichocerca cylindrica (Imhof)

The following species occur in the Douglas Lake plankton but are not discussed in this paper, either because of their scarcity or because of difficulty with identification in the counting cell:

Chromogaster ovalis (Bergendal)

Conochiloides dossuarius (Hudson)

Keratella quadrata (Müller)

Lecane luna (Müller)

Monostyla bulla Gosse

Monostyla lunaris (Ehrenberg)

Synchaeta oblonga Ehrenberg

Synchaeta pectinata Ehrenberg

Trichocerca pusilla (Jennings)

Trichocerca similis Wierzejski

Trichotria tetractis (Ehrenberg)

THERMO-CHEMICAL DEPRESSION INDIVIDUALITY

Douglas Lake is typically a temperate lake of the second order. Ice covers the lake from approximately early December to April. Continuous and strong winds usually extend the periods of vernal and autumnal circulation over four weeks or more and result in the establishment of a homothermous and essentially a homochemical condition. During the summer and early autumn this lake exhibits thermal stratification as evidenced by the existence of distinct thermoclines.

The discussion which follows is based upon data presented in Figures 2-5. Each set of graphs records the physical and chemical conditions within one depression, and is identified by the initials from the name of that depression and the month, day and year respectively of sampling. It should be noted that temperature and depth are so plotted that 1 unit ($1^{\circ}\text{C}.$) on the temperature scale is equivalent to 1 unit (1 meter) on the depth scale.

Throughout this paper the term *chemical stratification* is used to indicate that there exists for a particular chemical factor or factors a region of rapid and pronounced change, similar to the marked thermal changes that occur in the thermocline. Thus far no conventional rule has been adopted by limnologists

applying to chemical stratification in the same manner that Birge's rule applies to thermal stratification.

Because the physical and chemical data from 1938 are more complete, it will be the writer's practice to discuss them in detail and to include but brief comments concerning those of 1937.

THERMAL CONDITIONS

Stratification.

The only April record for 1938 is from South Fish-Tail depression (Fig. 3). It shows a homothermous condition with a difference of but $0.5^{\circ}\text{C}.$ between the surface and bottom temperatures. Although a considerable warming had occurred by May 14-15, the spring circulation was still extant. Of the three depressions studied at that time, South Fish-Tail alone showed a significant difference ($4^{\circ}\text{C}.$) in temperature between the bottom and surface waters. Thermal changes in the 15-17 meter water stratum were suggestive of a potential thermocline.

The upper and lower limits of the thermoclines in the various depressions are indicated by broken horizontal lines in Figure 6. As might be expected from its protected position, South Fish-Tail was the first depression to stratify, with the establishment by May 25 of a thermocline at 16-17 meters. In contrast, circulation was still active in Grapevine, Fairy

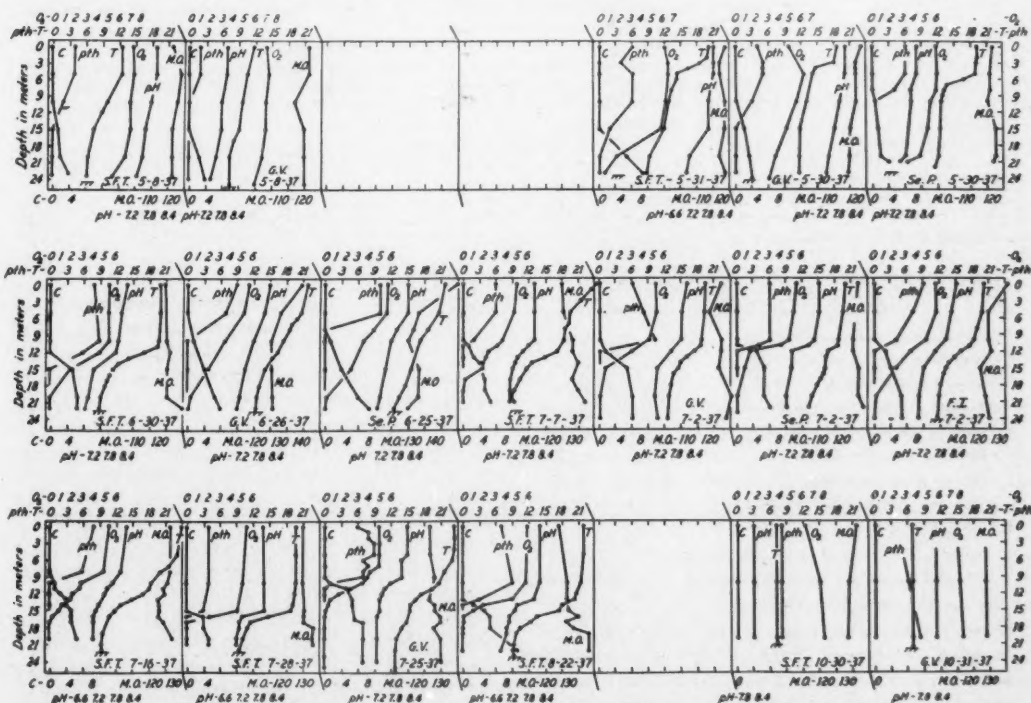


FIG. 2. Graphs showing vertical chemical and thermal variation in several of the Douglas Lake submerged depressions, 1937. Lake bottom indicated by ///.

Abbreviations: C., free carbon dioxide in ppm.; F.I., Fairy Island depression; G.V., Grapevine depression; M.O., methyl orange alkalinity in ppm. calcium carbonate; O_2 , dissolved oxygen in cc. per liter; pth, hydrogen-ion concentration; pth., phenolphthalein alkalinity in ppm. calcium carbonate; Se.P., Sedge Point depression; S.F.T., South Fish-Tail depression; T., temperature in degrees Centigrade.

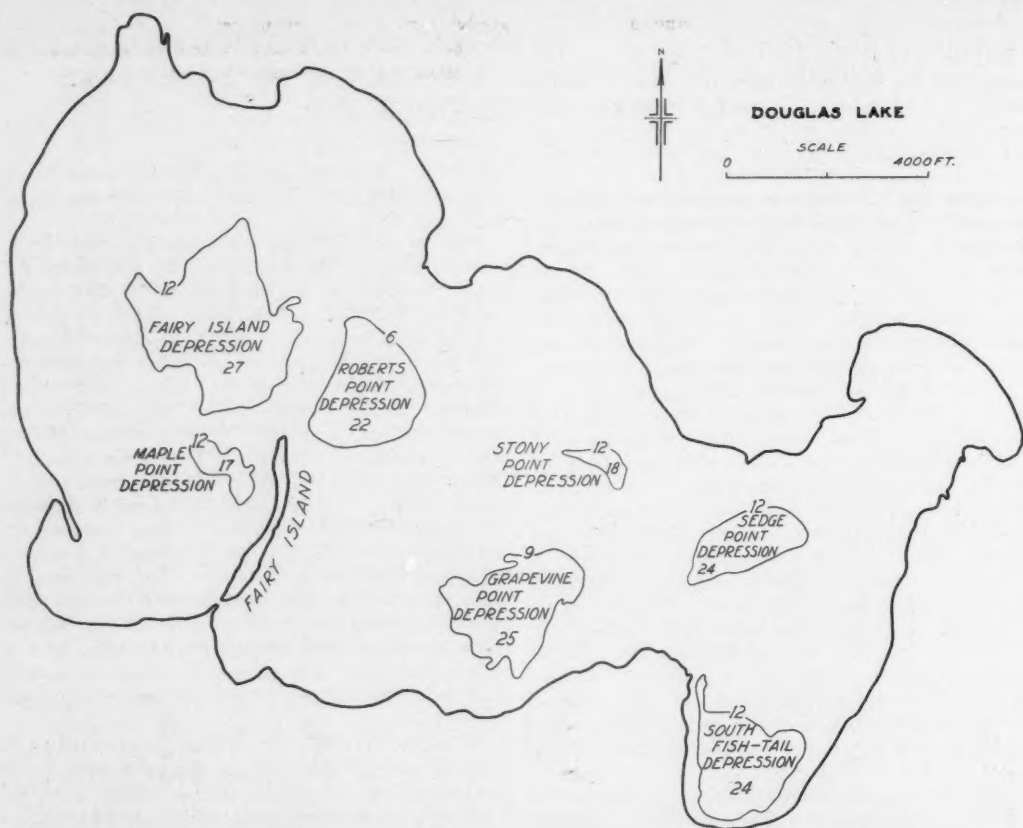


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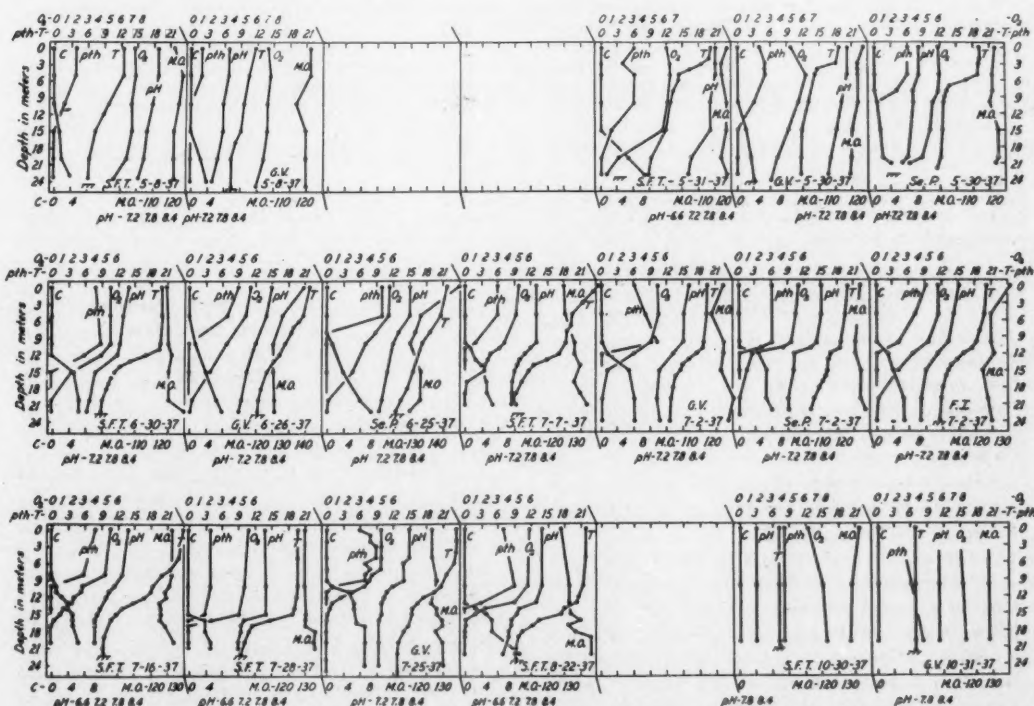
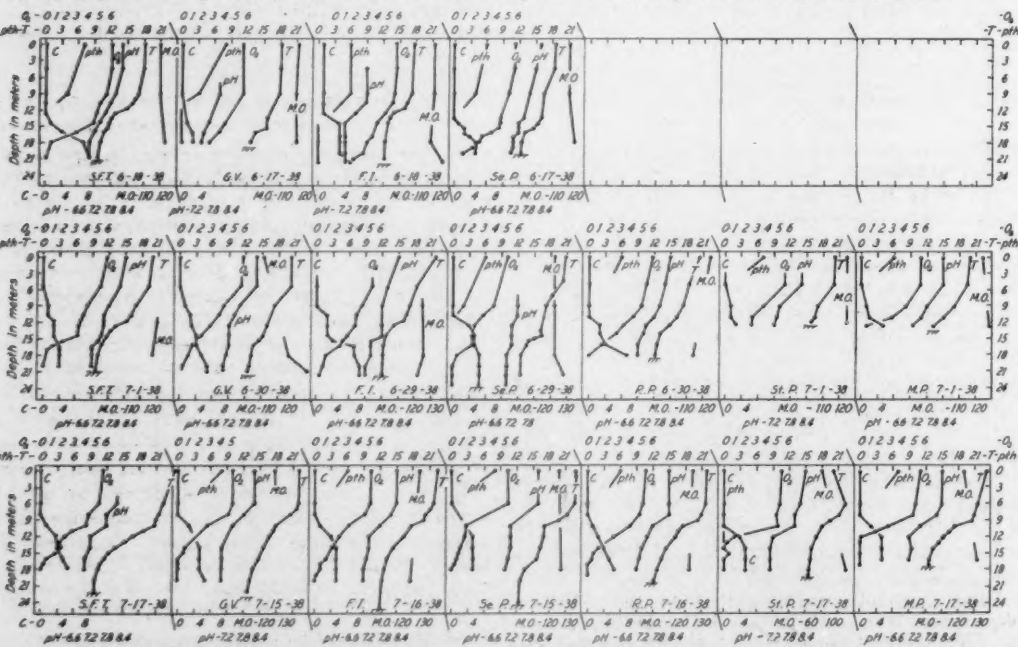


FIG. 2. Graphs showing vertical chemical and thermal variation in several of the Douglas Lake submerged depressions, 1937. Lake bottom indicated by ///.

Abbreviations: C, free carbon dioxide in ppm.; F.I., Fairy Island depression; G.V., Grapevine depression; M.O., methyl orange alkalinity in ppm. calcium carbonate; O_2 , dissolved oxygen in cc. per liter; pH, hydrogen ion concentration; pth, phenolphthalein alkalinity in ppm. calcium carbonate; Se.P., Sedge Point depression; S.F.T., South Fish-Tail depression; T., temperature in degrees Centigrade.



Abbreviations: *C.*, free carbon dioxide in ppm.; *F.I.*, Fairy Island depression; *G.V.*, Grapevine depression; *M.O.*, methyl orange alkalinity in ppm. calcium carbonate; *M.P.*, Maple Point depression; *O₂*, dissolved oxygen in cc. per liter; *pH*, hydrogen-ion concentration; *pth.*, phenolphthalein alkalinity in ppm. calcium carbonate; *R.P.*, Roberts Point depression; *Se.P.*, Sedge Point depression; *S.F.T.*, South Fish-Tail depression; *St.P.*, Stony Point depression; *T.*, temperature in degrees Centigrade.

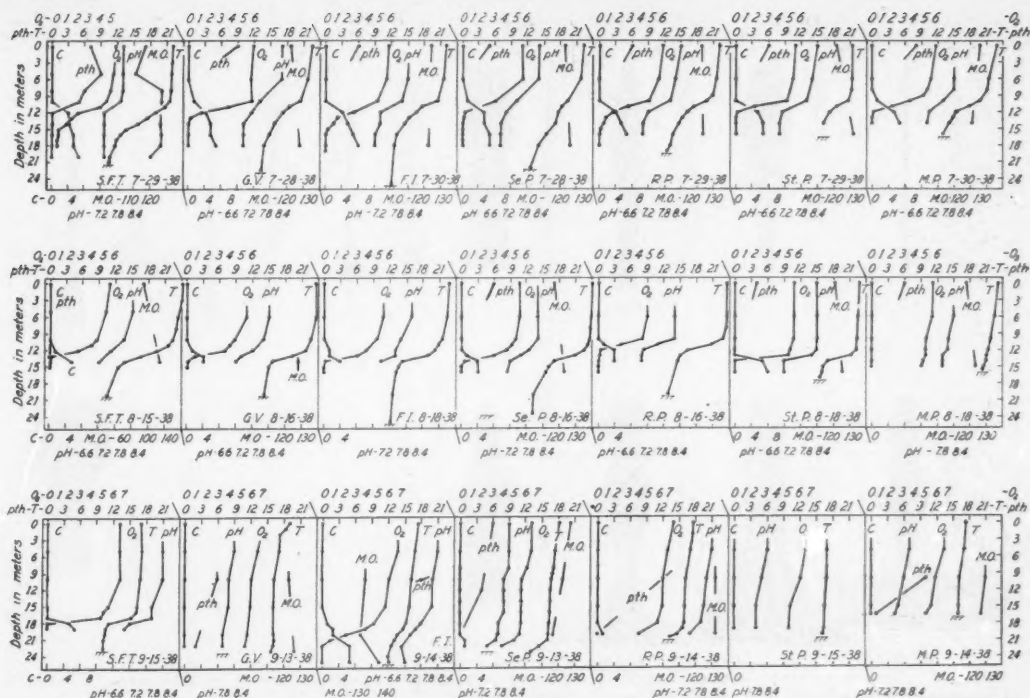


FIG. 5. Graphs showing vertical chemical and thermal variation in the seven submerged depressions of Douglas Lake, July 28 to September 13 inclusive. Lake bottom indicated by ///.

Abbreviations: C., free carbon dioxide in ppm.; F.I., Fairy Island depression; G.V., Grapevine depression; M.O., methyl orange alkalinity in ppm. calcium carbonate; M.P., Maple Point depression; O_2 , dissolved oxygen in cc. per liter; pH, hydrogen-ion concentration; pth., phenolphthalein alkalinity in ppm. calcium carbonate; R.P., Roberts Point depression; S.P., Sedge Point depression; S.F.T., South Fish-Tail depression; St.P., Stony Point depression; T., temperature in degrees Centigrade.

Island, Sedge Point and Maple Point depressions. By July 1, thermoclines were well established in the deeper depressions but were absent in the three shallower depressions. All depressions were thermally stratified by July 17 and so persisted through middle August, with the exception of Maple Point which lacked stratification on August 18. Early autumnal circulation depressed the thermoclines below their August level in South Fish-Tail, Fairy Island, Sedge Point and Roberts Point depressions, and eliminated thermal stratification in the other three depressions by September 15. Therefore it may be stated that, at least in 1938, thermal stratification was established on different dates in the several depressions, and in the autumn disappeared on different dates due to circulation differences among the depressions.

Figure 6 also indicates differences in depth levels at which the thermoclines exist. For instance, in the June 17-18 series, the extremes in depth levels of the lower limits of the thermoclines differed by 3.5 meters, and in the July 15-17 series by 6.5 meters. Similar differences exist among the depth levels of the upper thermocline limits. These differences were less marked in August as a result of more thorough and deeper circulation of the epilimnion waters. Still more vigorous circulation in September resulted in a

5-meter difference among the extremes of the lower thermocline limits in the three stratified depressions.

Further thermal differences among depressions are evident when thermocline widths are considered (Fig. 6). During June, thermoclines did not exceed 2 meters in width, so that little dissimilarity was discernible. However, by July 15-17 the thermocline in South Fish-Tail was 6 meters wide in contrast to a width of 1.5 meters in Grapevine and Roberts Point depressions. Thermocline widths in the other depressions varied between these extremes. Similar differences among depressions may be observed in late July, August and even in the September series.

Although the 1937 series showed similar variations among depressions, the dates of thermocline formation were different. Stratification occurred considerably earlier, being definitely established by the end of May. This stratification had disappeared from Grapevine and Sedge Point depressions by June 26-30, but persisted in South Fish-Tail. The autumnal overturn began at some time previous to October 30.

Bottom-water Temperatures.

Bottom-water temperatures for 1938 in all depressions appear in Table 1. They were different for each

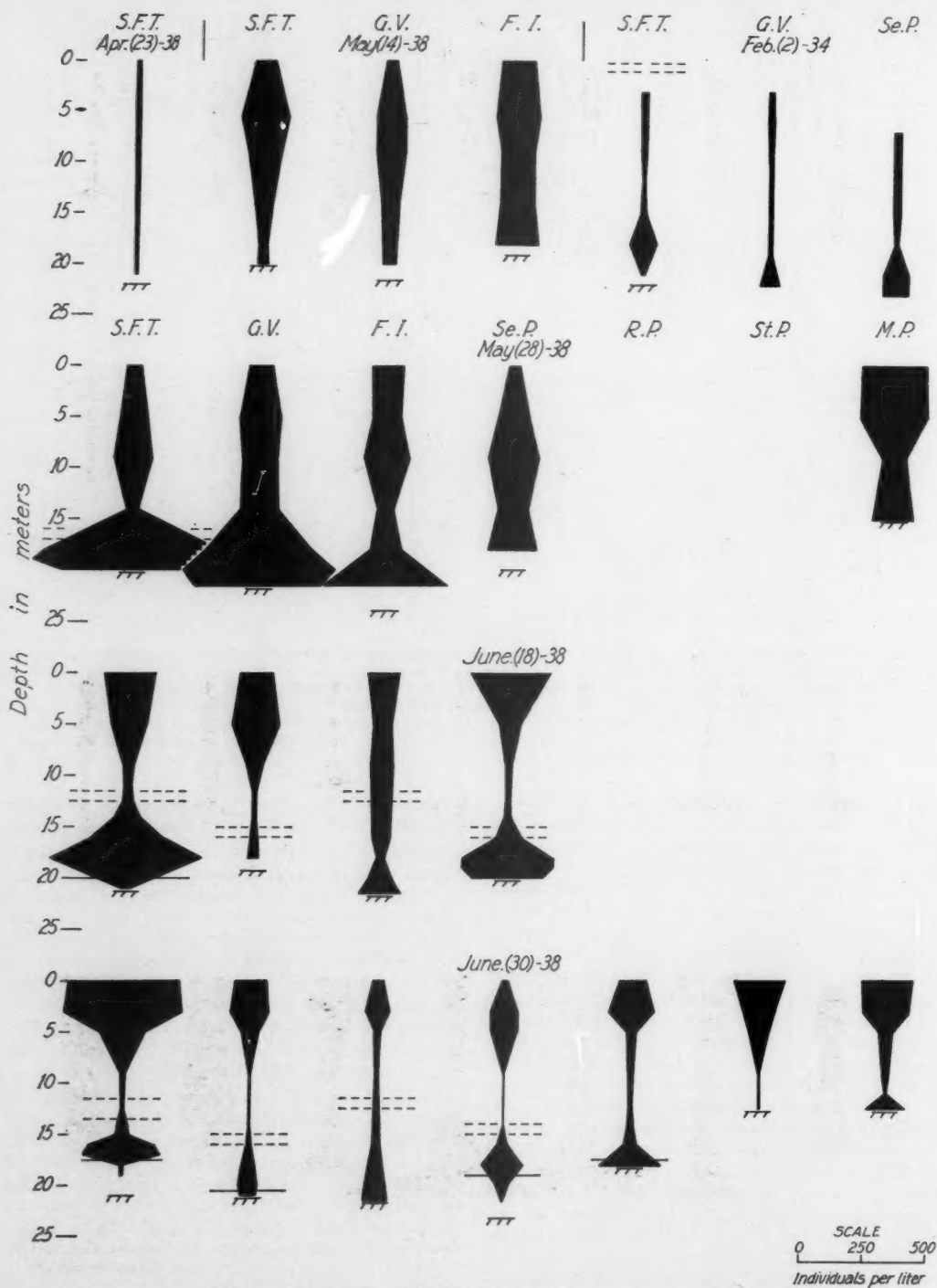


FIG. 6. Vertical distribution graphs of total Rotifera populations in each of the seven Douglas Lake depressions, 1938. Including February 1-3 series, 1934.

Broken horizontal lines indicate the upper and lower thermocline limits; solid horizontal lines, oxygen concentrations of 0.1 cc. per liter; figures in parentheses indicate that that series occupied approximately 3 days about the date designated; lake bottom indicated by ///.

Abbreviations: F.I., Fairy Island depression; G.V., Grapevine depression; M.P., Maple Point depression; R.P., Roberts Point depression; S.F.T., South Fish-Tail depression; Se.P., Sedge Point depression; St.P., Stony Point depression.

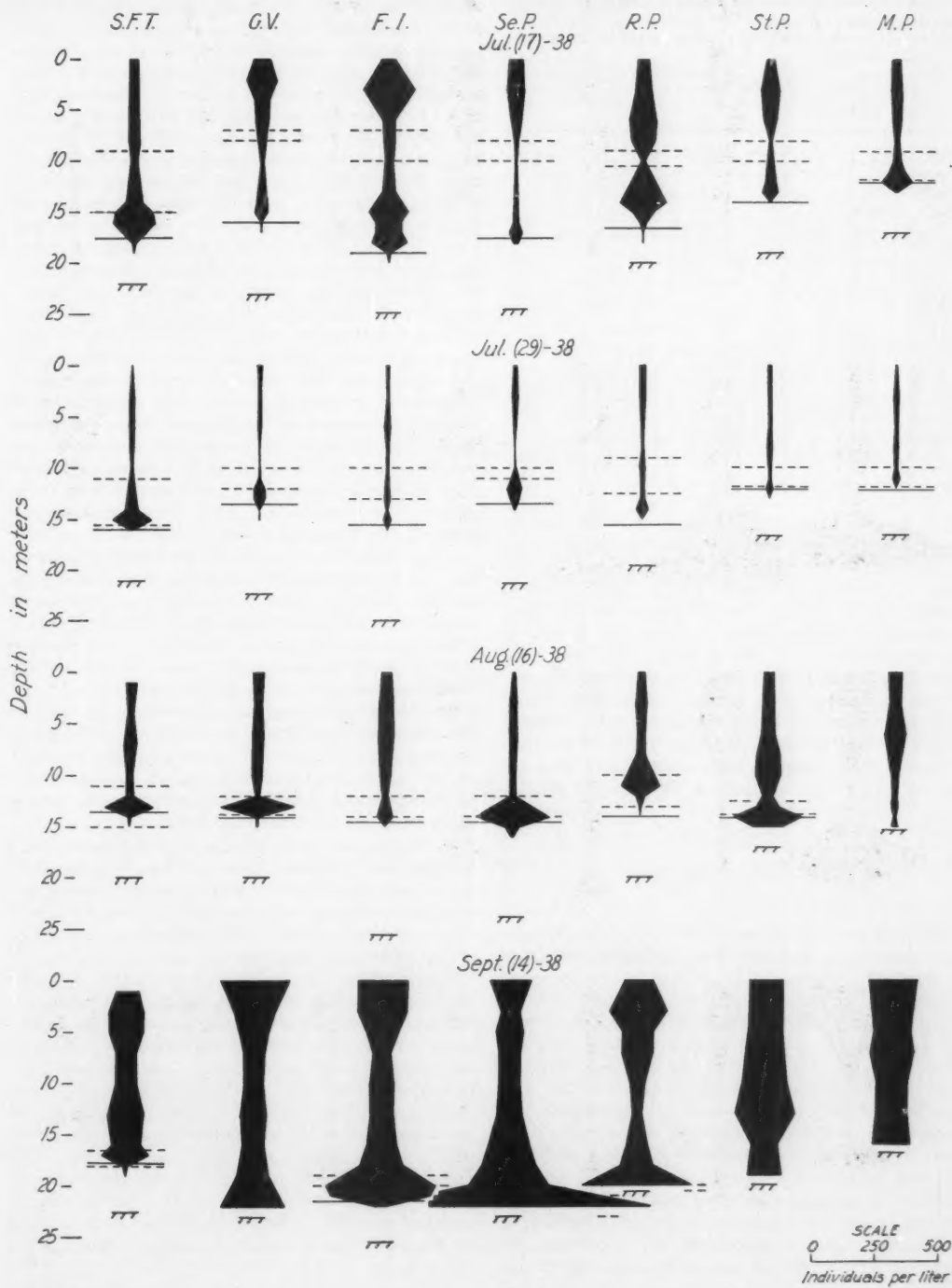


FIG. 6 (Continued)

TABLE 1. Bottom-water temperatures in °C. for Douglas Lake depressions, 1937, 1938. One asterisk indicates temperature record 1 meter above lake bottom; 2 asterisks, 2 meters above lake bottom.

Abbreviations: *F.I.*, Fairy Island depression; *G.V.*, Grapevine depression; *M.P.*, Maple Point depression; *R.P.*, Roberts Point depression; *S.F.T.*, South Fish-Tail depression; *Se.P.*, Sedge Point depression; *St.P.*, Stony Point depression.

Date	S.F.T.	G.V.	F.I.	Se.P.	R.P.	St.P.	M.P.
1937							
5-8....	6.4*	7.5*					
5-30-31.	8.6	11.5*		11.4*			
6-25-30.	9.0	12.4		12.5			
7-2-7.	9.4*	12.4*	11.4*	13.0			
7-25-28.	9.6	13.3					
10-30-31.	7.2	6.8					
1938							
5-14-15.	8.3*	11.4*	11.7*				
5-28-29.	8.5*	12.3*	11.9*	12.4*			12.3*
6-17-18.	9.5*	12.7*	12.2*	12.4			
6-29-30.	9.6	12.5	12.1	12.5**	12.2	15.9*	13.3*
7-15-17.	9.9	12.9*	12.0	12.5	12.2	15.6	12.6
7-28-30.	10.4	13.3	12.0	12.6	12.4	16.1**	12.9
8-15-18.	10.3	14.1	12.2	13.1	12.9	15.5	20.4
9-13-15.	10.0	15.8	12.2	13.0	13.3	16.2	16.0

depression on all corresponding dates. The greatest temperature difference on corresponding dates among all depressions amounted to 10.1°C., among depressions of comparable depths 5.8°C. Early thermal stratification in South Fish-Tail depression prevented a warming of its hypolimnion comparable to that of the other depressions. As a result, this depression showed the lowest bottom-water temperatures throughout the entire stagnation period. In contrast, Stony Point depression which was one of the last to stratify thermally, had the highest average bottom-water temperature. The unusually high bottom-water temperature of 20.4°C. in the shallow Maple Point depression, August 18, was due to an early overturn occasioned by continuous northwest winds.

CHEMICAL CONDITIONS

Dissolved Oxygen.

The epilimnion is common to all of the Douglas Lake depressions and therefore but slight differences in dissolved oxygen (O_2) are here to be expected within any series. In general, the epilimnion of Douglas Lake gradually warms, with the accompanying reduction of O_2 , until about the end of July. From this time on, until the surface water freezes, there is an increase in the O_2 correlated with temperature decrease. In contrast to this stratum, the hypolimnion and thermocline are regions of significant variation with respect to O_2 content and they will now be discussed in some detail.

With the establishment of stratification, the hypolimnion is shut off from the circulating influences of wind action and the accompanying continuous O_2 replenishment. However, the various O_2 -reducing factors in the lowermost region continue their inroads upon the supply of O_2 . In 1937 and 1938 practically the entire hypolimnion became devoid of O_2 by the middle of August (Figs. 2, 5). This O_2 exhaustion

of the hypolimnion in Douglas Lake may occur as early as the middle of July.

Since South Fish-Tail depression is the first to stratify, it is the first of the depressions to give any indication of O_2 reduction in the hypolimnion. This is evident from the series of May 14-15 and again in the May 28-29 series (Fig. 3). By June 18 the O_2 had gone from the lower hypolimnion in this depression (Figs. 4, 6). The other depressions showed a definite decrease in O_2 on this date, but in none of them had the O_2 been reduced to below 0.8 cc. per liter. By July 1 two of the seven depressions lacked O_2 in the lowermost waters of the hypolimnion and two others had O_2 concentrations less than 0.1 cc. per liter at this depth. The remaining depressions possessed bottom O_2 concentrations of 0.3, 0.5 and 2.4 cc. per liter. Thus it is evident that the rate of O_2 depletion is different in the several depressions. This fact is further supported if the depth levels of the solid horizontal lines in Figure 6 are compared. These lines represent O_2 concentrations of 0.1 cc. per liter. It will be observed that, in the series of June 29-30, O_2 depletion was most extensive in South Fish-Tail and became less so in the several depressions in the following order:—Sedge Point, Grapevine and Roberts Point. In Fairy Island depression the O_2 concentration at the bottom still exceeded 0.1 cc. per liter. By July 29 however, O_2 depletion in Grapevine, Sedge Point and Fairy Island had progressed far beyond that in South Fish-Tail, while in Roberts Point depression O_2 depletion was of the same magnitude as that in South Fish-Tail.

The staggering of the solid horizontal lines in any one series in Figure 6 is ample evidence of the different depth levels at which O_2 concentrations equal 0.1 cc. per liter; or of the fact that O_2 concentrations at similar depth levels differ greatly in the several depressions on corresponding dates.

In the August series, Figure 6, it will be observed that the solid horizontal lines are less staggered than in the preceding series. This somewhat greater uniformity in the O_2 conditions in all depressions is due, in the main, to the more vigorous circulation of the epilimnion by that date.

Consideration of the September series indicates that replenishment of the O_2 supply occurs on very different dates and at varying rates in the depressions. South Fish-Tail and Fairy Island depressions at this time lacked dissolved O_2 in the bottom 4.5 and 3 meters respectively. In Sedge Point and Roberts Point depressions dissolved O_2 was less than 3.8 cc. per liter at the bottom, indicating that circulation was still incomplete. Oxygen concentrations were approaching saturation values in the remaining depressions. It should be noted that partial saturation had occurred in Maple Point depression as early as August 16 due to an early overturn in that shallow depression.

With reference to the zone of abrupt population change in the plankton Rotifera, the region of rapid O_2 decline is probably as significant as the level of actual O_2 exhaustion. This region of rapid O_2 de-

eline is close to the bottom during the period of early thermal stratification, but, as the layer of oxygenless water increases in thickness, it gradually moves upward. However, not until late July did it become coincident with the lower thermocline level. In the August series the thermoclines and the strata of marked O_2 decline were finally identical (Fig. 6). This relation of O_2 and thermal stratification will be considered again in a later section of the paper. At this point it should be stated that the stratum of marked O_2 decline varied in thickness and in the depth at which it was found in the seven depressions on all corresponding sampling dates. This statement is based upon the data presented in Figures 2-5.

Free Carbon Dioxide.

Circulation of the water during the spring and fall overturns results in the disappearance of free carbon dioxide (CO_2) at all depths. This condition continues to prevail in the epilimnion throughout the summer stagnation period. In the hypolimnion, however, a gradual accumulation of free CO_2 begins with the establishment of thermal stratification. A comparison of the graphs of free CO_2 and O_2 in Figures 2-5 will show a pronounced interrelationship between the amounts of these gases present at any one time. When the quantities of O_2 are high, the free CO_2 is low, and as the O_2 content decreases the free CO_2 content shows a corresponding increase. Moreover, the region of rapid O_2 decline coincides with the stratum of rapid free CO_2 increase, so that the curves representing the vertical distribution of these gases may be considered as complementary. Since the foregoing section has presented evidence of depression individuality with respect to O_2 , it then follows that a similar depression individuality exists for free CO_2 . The free CO_2 values presented in Table 2 are selected as one brief means of expressing depression individuality. However, it should be understood that values from other levels in the region of distinct CO_2 change within the hypolimnion yield corroborative evidence.

The greatest differences in free CO_2 concentration among the depressions are observable in the spring and early summer and in the autumn before all of the depressions have been completely mixed. Similar differences in the amounts of free CO_2 may be observed in the 1937 records (Fig. 2).

TABLE 2. Comparison of free CO_2 in ppm. at 18 meters depth in six submerged depressions, Douglas Lake, 1938.

Abbreviations: *F.I.*, Fairy Island depression; *G.V.*, Grapevine depression; *R.P.*, Roberts Point depression; *S.F.T.*, South Fish-Tail depression; *Se.P.*, Sedge Point depression; *St.P.*, Stony Point depression.

Date	S.F.T.	G.V.	F.I.	Se.P.	R.P.	St.P.
5-14-15...	4.0	0.0	0.0			
5-28-29...	2.0	trace	0.0	0.0		
6-17-18...	7.0	2.0	3.0	4.0		
6-29-30...	3.0	4.0	7.0	5.0	7.0	
7-15-17...	5.0	4.0	4.0	4.0	5.0	4.0
7-28-30...	4.0	5.0	5.0	5.0		
9-13-15...	4.0	0.0	1.0	0.0	0.0	0.0

Hydrogen-ion Concentration.

Douglas Lake is distinctly alkaline with respect to hydrogen-ion concentration. Even during summer stagnation the pH of the bottom waters only occasionally reaches 6.8. The pH of the surface waters normally varies around 8.2. The fact that even in the absence of free CO_2 the hydrogen-ion concentration in the deeper water gradually approaches neutrality indicates that the pH is but partially dependent upon the presence of dissolved CO_2 . However, it is evident from an inspection of Figures 2-5 that any pronounced changes in the hydrogen-ion concentration are coincident with pronounced changes in the amounts of free CO_2 . Further, these changes differ among depressions.

The pH values presented in Table 3 are selected as one brief means of expressing depression individuality. However, it should be understood that values from other levels in the region of distinct pH change within the hypolimnion yield corroborative evidence.

TABLE 3. pH records from 18 meters depth in several Douglas Lake depressions, 1938.

Abbreviations: *F.I.*, Fairy Island depression; *G.V.*, Grapevine depression; *R.P.*, Roberts Point depression; *S.F.T.*, South Fish-Tail depression; *Se.P.*, Sedge Point depression; *St.P.*, Stony Point depression.

Date	S.F.T.	G.V.	F.I.	Se.P.	R.P.	St.P.
5-14-15...	7.3	8.0	8.0			
5-28-29...	7.5	7.8	7.8	7.8		
6-17-18...	7.0	7.3	7.2	7.2		
6-29-30...	7.0	7.1	7.2	7.0	7.0	
7-15-17...	7.0	7.0	7.0	7.0	7.0	7.1
7-28-30...		7.0	7.0	7.0		
9-13-15...	7.0	7.8	7.6	7.8	7.8	7.8

The gradual approach of the hypolimnion to a condition of neutrality is clearly shown. That this tendency leads to similarities in the hydrogen-ion concentrations in the depressions as summer stagnation progresses is evident from the July series. The September records reflect the effects of the fall overturn, namely, the return of the hypolimnion to a condition of distinct alkalinity.

Alkalinity.

Alkalinity is recorded as phenolphthalein alkalinity and methyl orange alkalinity in ppm. of calcium carbonate. Reasonably complete analyses in 1937 (Fig. 2) failed to show any evidence of an alkalinity stratification coinciding with the zones of fluctuation in the rotifer population. Therefore, throughout 1938, determinations were often restricted to surface and bottom samples.

Phenolphthalein alkalinity in ppm. shows very little variation among depressions, especially when the uncertainty of the endpoint in this titration is considered. Excepting the periods of active circulation, there is a gradual decrease in the titration values from the surface to the upper level of the thermocline where samples invariably fail to show any color change.

The methyl orange alkalinity in ppm. was found to be quite variable in Douglas Lake. In some series but slight differences appeared between the surface and bottom, while in others differences of 10 to 25 ppm. occurred. Likewise there were no consistent vertical changes, but rather an irregular variation from surface to bottom. In many instances differences were apparent among depressions.

WINTER RECORDS

In the winter records from South Fish-Tail depression (Fig. 3) the O_2 in water deeper than 15 meters showed a noticeable decrease by February. However, there still remained 0.2 cc. per liter of O_2 in the water 1 meter above the bottom in early April. The free CO_2 increased during this time to 12 ppm. 1 meter from the bottom. A thin thermocline developed by February, extending from surface to 1 meter depth only.

DEPRESSION INDIVIDUALITY WITH RESPECT TO VERTICAL DISTRIBUTION OF THE ROTIFERA

Prior to the detailed discussion of the faunal aspect of this problem, it will be necessary to comment upon a few of the more apparent facts of rotifer distribution in Douglas Lake. During the autumn and spring overturns the Rotifera are distributed with reasonable uniformity from surface to bottom. As stagnation sets in, they gradually disappear from the deeper water as this region becomes devoid of O_2 and congregate in the upper water strata. Thus it is common, in the regions of rapid O_2 decline, where O_2 may drop from 3.0 to less than 0.1 cc. per liter, to find distinct concentration zones in the rotifer population.

Intensive consideration of differences among depressions in the vertical rotifer distribution within the epilimnion was not attempted in this work since submerged depression individuality as already known for Douglas Lake concerns primarily the thermoclines and hypolimnions. The sampling throughout the epilimnion was done primarily to have information on any distributional phenomena in its lower regions which might have a significant bearing on the main problem.

EVIDENCE FROM POPULATION TOTALS

Total Rotifera populations in the seven Douglas Lake depressions, April-September, 1938, and February 1-3, 1934, are presented graphically in Figure 6. Each pattern is drawn quantitatively to scale and represents the vertical distribution of total Rotifera in one depression. Comparison of these figures within any one series will indicate marked distributional differences, which are considered by the author as evidence of a distinct depression individuality with reference to rotifer distribution. The nature of these differences will now be discussed in some detail.

The presence of marked concentration zones in the rotifer population below 15 meters in three of the depressions, May 28-29, and the absence of same in Sedge Point and Maple Point depressions, indicates

that near the conclusion of the spring overturn concentration zones are established on different dates in the several depressions. Likewise, near the termination of the summer thermal and chemical stratification period, concentration zones disappeared from depressions on different dates. Thus in the September series, while marked concentration zones were found in Fairy Island, Sedge Point and Roberts Point and less definite zones in South Fish-Tail and Grapevine, they were absent from Stony Point and Maple Point depressions. The concentration zone had disappeared from Maple Point depression prior to August 16.

Once established, the concentration zones exist at decidedly different depth levels in the several depressions. For example, in the series of July 15-17, a concentration zone was found at 12 meters in Maple Point, 13 meters in Stony Point, 14 meters in Roberts Point, 15 meters in Grapevine and 15-16 meters in South Fish-Tail depression. Sedge Point depression showed a concentration zone at 17 meters and Fairy Island at 15-18 meters. It will be noticed that as the stagnation period progressed these concentration zones moved nearer to the surface, but still maintained these differences in depth location. Thus in late July, when all of the concentration zones were at least 1 meter nearer to the lake surface and in Sedge Point depression 5 meters nearer the lake surface, the concentration zones were located as follows: Maple Point, 11 meters; Stony Point, 12 meters; Roberts Point, 14 meters; Grapevine, 12.5 meters; South Fish-Tail, 15 meters; Sedge Point, 12.5 meters; and Fairy Island, 15 meters. Even in the August 15-18 series where the concentration zones would seem to be trapped between the circulating epilimnion and the ever-widening stratum devoid of O_2 , differences in depth locations of these zones were still apparent. Similar differences will be noted in the winter series, February 1-3, 1934. On that date South Fish-Tail, Grapevine and Sedge Point depressions showed concentration zones at 18, 22 and 21-23 meters respectively.

The extent or widths of the concentration zones likewise varied among depressions on corresponding dates. Although the nature of these zones precludes setting definite delimiting levels, approximations may be stated. In the series of June 17-18, these zones were 4 meters, 2-3 meters and 2 meters in width in South Fish-Tail, Sedge Point and Fairy Island depressions respectively. Comparable dissimilarities are also observable June 29-30. In the series of July 15-17, relatively wide zones were found in South Fish-Tail, Fairy Island and Roberts Point depressions, and quite narrow zones in the remaining depressions.

The magnitude of the population concentration zones may be determined by comparison of the distribution patterns with the scale given in Figure 6. Once again decided differences are observable among depressions. For instance, on June 17 and 18, the greatest number of individuals in the concentration zones were 590, 360, 150 and 40 per liter in South

Fish-Tail, Sedge Point, Fairy Island and Grapevine respectively. Corresponding differences will be apparent on all other dates of sampling. The largest number of individuals recorded in 1938 was 1,110 per liter at 22 meters in Sedge Point depression, September 13.

A further indication of depression individuality with respect to rotifer distribution will be seen if the extent of the regions of the hypolimnion lacking rotifer populations are considered on comparable dates. Variations among depressions in the vertical extent of those unlinked portions which extend from the concentration zones to the lake bottom are quite apparent.

Similar differences were discernible among the depressions in the 1937 data. For example, on July 25 and 28, there was a difference of 2.5 meters between the depth levels of the concentration zones in South Fish-Tail and Grapevine depressions.

EVIDENCE FROM SPECIES

Species distribution presents differences between depressions comparable to those presented for the rotifer population totals. The vertical distribution data by species for 1937, 1938 and the winter of 1933-34 are on file in the Horace H. Rackham School of Graduate Studies, University of Michigan. The following discussion is based upon those data. The few species here described were selected as representative of the more numerous ones in the plankton collections.

Polarthra euryptera showed a concentration zone from 15-16.5 meters in South Fish-Tail and from 12-14 meters in Grapevine depression on July 28, 1937. During July 15-17, 1938, these concentration zones occurred from 8-17 meters in South Fish-Tail; 8-18 meters in Fairy Island; and 10-13 meters in Stony Point depression. In the other depressions on this date concentration zones were absent.

Keratella cochlearis, the most numerous of the Douglas Lake plankton rotifers, indicated rather striking depression individuality with respect to its vertical distribution. From May 30-31, 1937, concentration zones were well established at 5-20 meters in South Fish-Tail, at 10-23 meters in Grapevine and at 8-20 meters in Sedge Point depression. Although large numbers occurred at all depths in September, 1938, concentration zones in the various depressions were apparent as follows: South Fish-Tail, 13-17 meters; Grapevine, 19-22 meters; Sedge Point, 16-22 meters; Roberts Point, 18-20 meters; Stony Point, 10-19 meters; and Maple Point, 7-16 meters.

Kellicottia bostoniensis was the only abundant rotifer confined to the hypolimnion. Population differences in this species illustrate especially well this depression individuality. On July 25 and 28, 1937, concentration zones were found at 16-17.5 meters in South Fish-Tail, and at 12 and at 14 meters in Grapevine depression. In August, 1938, similar zones existed at 11 meters in Roberts Point; at 13 meters in South Fish-Tail, Grapevine and Sedge Point; at 14 meters in Fairy Island; and at 14-15 meters

in Stony Point depression. No concentration zone was present in Maple Point depression. In September, such zones were absent in Maple Point, Stony Point and South Fish-Tail depressions. They were present, however, in Roberts Point, Fairy Island, Grapevine and Sedge Point depressions at 20, 20-21, 22 and 22 meters respectively.

The preceding information is illustrative of species dissimilarities in depth locations and in widths of concentration zones. Certain other distinct quantitative dissimilarities will now be considered. *Kellicottia bostoniensis* showed in the series of June 29-30, 1938, a maximum population in South Fish-Tail depression of 74 individuals per liter at 17 meters, but failed to exceed 4 individuals per liter at any depth in the other depressions. Likewise on July 28-30, this species numbered 101 individuals per liter in South Fish-Tail and failed to exceed 26 per liter in the other depressions at any depth. Records for June 17-18 and July 15-17 suggest similar situations. In contrast, the same species was abundant August 15-18 in all depressions except Maple Point.

In general, if the individuals of a species were numerous in one depression they were found in all other depressions, even though frequently in varying numbers. No marked examples of qualitative differences among depressions were observed. In species numbering less than 10 per liter, individuals were frequently found in several depressions and absent from the others. Such differences were not found to be constant, and were not considered to be significant.

The population differences among depressions, as presented in this section or as indicated in Figure 6, are considered by the writer to establish depression individuality with respect to vertical distribution of the plankton Rotifera in Douglas Lake, at least for the years 1937, 1938 and the winter of 1933-34.

SEASONAL VARIATION IN VERTICAL DISTRIBUTION

DISTRIBUTION OF TOTAL ROTIFERA

Graphs of the vertical distribution of total Rotifera, April-September, 1938, and February, 1934, are presented in Figure 6. The horizontal broken lines represent upper and lower thermocline limits and the solid horizontal lines, O_2 concentrations of 0.1 cc. per liter. Graphs presenting more complete thermal and chemical data on similar dates are shown in Figures 2-5. Although distributional differences as were discussed in the preceding section are apparent among depressions, they do not mask the broader seasonal changes now to be discussed.

During the vernal and autumnal overturn periods, the vertical rotifer distribution is more uniform than at any time during thermal and chemical stratification. The April 23 graphs indicate a uniform surface-bottom distribution. In the May 14-15 series, when, with the exception of South Fish-Tail depression, circulation was still active, distribution was less uniform but was still distinctly different from the

distributional patterns of the stagnation periods. Likewise Stony Point and Maple Point depressions, September 13-15, showed evidence of the more uniform distribution characteristic of the autumnal overturn period. A series from South Fish-Tail and Grapevine depressions, October 30-31, 1937, taken during circulation, showed a striking uniformity similar to that pictured for April, 1938. This uniformity is, without doubt, a result of the circulating water and the accompanying thermal and chemical surface-bottom uniformity.

Indications of approaching thermal and chemical stratification are recognized in the first temperature differences between surface and bottom waters; and in the lower hypolimnion—decrease in O_2 , appearance of CO_2 , and an increase in the hydrogen-ion concentration. Coincidental with this, rotifer concentration zones make their appearance in the water strata adjacent to the bottom. These conditions may be observed in the May 29-30 series. A similar condition was found in a series from South Fish-Tail, Grapevine and Sedge Point depressions, May 25-30, 1937. Likewise in Grapevine, Sedge Point and Roberts Point depressions, September 13-15, 1938, where incomplete circulation had eliminated the thermoclines but had not yet removed all traces of chemical stratification from the deeper waters, rotifer concentration zones were still present.

By June 18, although the distributional patterns were quite changed, typical concentration zones were found close to the bottom. It will be noticed that the lower thermocline levels were several meters above these zones. On the other hand the chemically stratified regions were, like the concentration zones, adjacent to the bottom.

The progressive upward-migration of the concentration zones in South Fish-Tail and Sedge Point depressions on June 17-18 and June 29-30, is typical of the distributional changes to follow throughout the remainder of the stratification period. This migration appears to be related to the O_2 decrease in the deeper water (solid horizontal lines indicate levels of O_2 concentration of 0.1 cc. per liter, Fig. 6). As the width of the oxygenless region increases, the rotifers become crowded into the ever-narrowing superimposed stratum. Thus by August 18, practically the entire rotifer population was confined to the upper 15 meters, that is, to the thermoclines and epilimnions. By this date the hypolimnions were almost entirely devoid of O_2 . It will be noticed that the concentration zones persisted throughout the stratification period.

The uniformity of the autumnal distribution continued into the period of ice cover. This was indicated by samples from South Fish-Tail depression taken November 24, 1933. However, coincident with O_2 decline, rotifer concentration zones appeared in the lower hypolimnions. The series of February 1-3, shown in Figure 6, indicates these typical concentration zones. Chemical records from South Fish-Tail (Fig. 3) showed these population zones to be within

the region of chemical stratification. The last 1934 plankton series to be taken through the ice indicated a distinct concentration zone at 20 meters, in the region of marked O_2 decline. Thus it is apparent, at least for the winter of 1933-34, and for the summers of 1937 and 1938, that typical concentration zones form within the hypolimnions both during the summer and winter stagnation periods. In contrast, a general uniformity in vertical distribution characterizes both spring and autumn overturns. Seasonal changes in vertical distribution as here recorded for the Rotifera are similar to those cited for zooplankters in general in the Wisconsin lakes by Birge and Juday (1911).

In the preceding paragraphs O_2 decrease has been presented as one environmental phenomenon closely associated with rotifer vertical distribution. The location of the concentration zones immediately above the levels of O_2 exhaustion places these zones almost invariably within the regions of rapid O_2 decline. In fact, these were so closely related that predictions of the depth locations of concentration zones could be made from a knowledge of O_2 distribution. Laboratory counts later invariably substantiated these predictions. Only one outstanding departure from this condition was found. This occurred in Stony Point depression, August 18, when the concentration zone extended into the region devoid of O_2 . Here the O_2 decreased from 4.8 to 0.0 cc. per liter within 1 meter and the Rotifera increased from 94 to 272 individuals per liter. In contrast, in South Fish-Tail depression, September 15, with a similar decrease in O_2 , the Rotifera decreased from 183 to 18 individuals per liter. The last mentioned change is rather representative of population changes found in the transition region from a zone of reduced O_2 supply to a zone of O_2 exhaustion. A few individuals, however, may occur in the upper levels of the regions devoid of O_2 . Rotifera were absent from the deeper regions of this stratum which had been devoid of O_2 for a longer time.

A relation between the O_2 conditions and the rotifer distribution, similar to that previously described for Douglas Lake, has been found by the author both in Hessler and Lancaster Lakes, Michigan. Birge and Juday (1911) state that zooplankters continue to occupy the lower strata in considerable numbers until the quantity of O_2 becomes too small for them, that is, less than 0.2 cc. per liter of water. This was generally true for the Rotifera of Douglas Lake. However, as pointed out in the preceding paragraph, rotifers frequently occurred in strata where O_2 had been reduced to below 0.1 cc. per liter, and occasionally even in the region of O_2 exhaustion.

In an earlier section it was pointed out that O_2 and CO_2 concentrations may be considered as complementary. Likewise pH was shown to be closely correlated with CO_2 content. It then follows that rotifer distribution- CO_2 and rotifer distribution-pH relationships exist, similar to the previously cited rotifer- O_2 relationships. The individual influences

of each of these factors were not separated in this study.

Temperature may be a factor in distribution, since these concentration zones were present in cooler water strata. Whether the concentration zones form solely as a result of migration from the ever-widening stratum of O_2 depletion or whether they result partly from that and in part from the seeking of certain optimal thermal and chemical conditions cannot be stated. It is apparent however, that the levels of significant population change in rotifer distribution are usually not within the thermoclines. Figure 6 indicates that during most of the stratification period concentration zones exist deeper than the thermoclines, and that little or no distributional changes occur within this stratum of rapid temperature change. This is of interest since some of the plankters may form concentration zones in the thermocline (Weleh 1935).

No relation was found between rotifer distribution and methyl orange and phenolphthalein alkalinities.

Inspection of Figures 2-5 and Figure 6 shows that, prior to August, thermal and chemical stratification were extant at different depth levels. During the same period the zones of pronounced change in rotifer population were closely associated with chemical stratification. In conclusion, it must be stated

that only certain of the factors important in vertical distribution could be considered in this investigation. Weleh (1935) lists light, food, dissolved gases, principally oxygen, and other dissolved substances, temperature, wind, gravity, and age of individuals of a species among the various influences operating in the production of various forms of vertical distribution.

SPECIES DISTRIBUTION

Certain characteristics of the distribution patterns of rotifer totals (Fig. 6) are in part due to the distinct distributional patterns of the more abundant species. That is, certain species are, in the main, responsible for the surface or near-surface concentration zones, and certain deep-water species form the bulk of the concentration zones within the hypolimnion. Figure 7 illustrates the seasonal changes in vertical distribution of the five most abundant species in South Fish-Tail depression. As previously indicated, distribution patterns vary among depressions, but these differences do not mask the broader seasonal changes. It will be observed that, in general, the distribution patterns in Figure 7 are similar to those for rotifer totals. During spring circulation, distribution is more nearly uniform than during the stratification period, except in those instances where the number of individuals does not exceed 5 per liter. By May 28, definite concentration zones had ap-

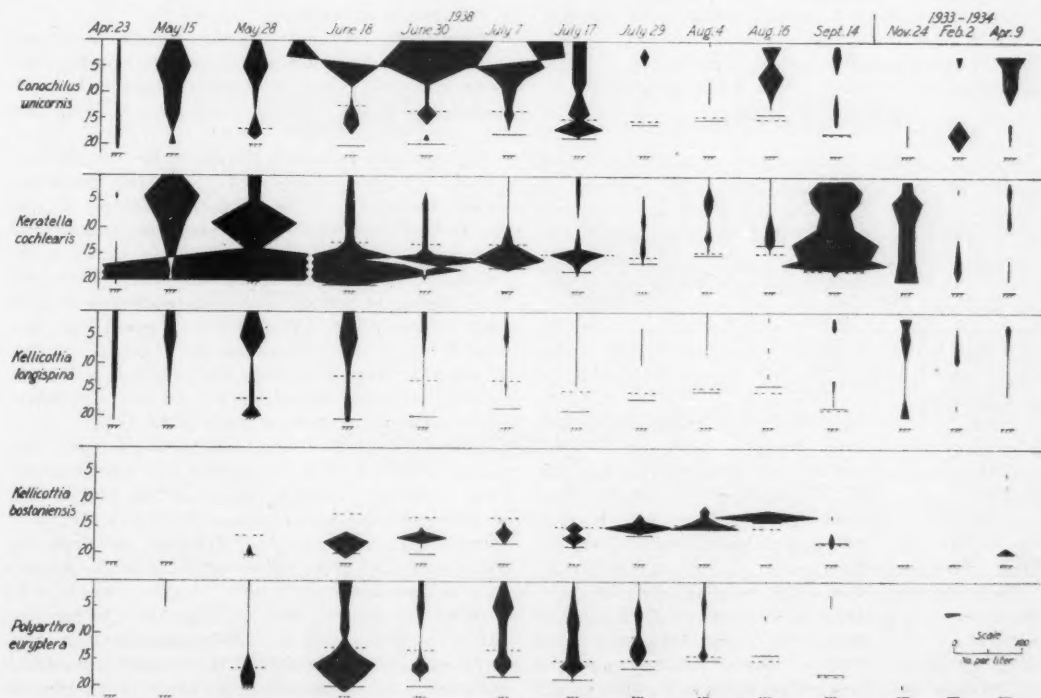


FIG. 7. Graphs showing seasonal changes in vertical distribution of the 5 most abundant rotifers in Douglas Lake plankton. Data from South Fish-Tail depression, April-September, 1938, and November-April, 1933-34. Depth indicated at 5-meter intervals for each species on left of figure. Broken horizontal lines represent lower limits of thermoclines; solid horizontal line, O_2 concentration of 0.1 cc. per liter; /// lake bottom.

peared near the bottom. These zones for most of the species persisted throughout the period of stratification; South Fish-Tail, it will be remembered, being definitely stratified in September. Winter records taken under the ice cover indicate the presence of concentration zones. It will further be observed that as stagnation progressed, the species moved away from the bottom, being restricted to the upper strata supplied with dissolved O_2 .

Conochilus unicornis. Typical concentration zones present throughout May, June and early July. Marked increase in numbers during June and early July confined to the epilimnion. February series, 1934, showed concentration zones adjacent to bottom.

Keratella cochlearis. In contrast to the preceding species, great increases in the population occurred within and, excepting September, restricted to the hypolimnion. In early May, September and November numerous also in epilimnion. Slight concentration zones in February.

Kellicottia longispina. Distribution rather uniform April-September. During July, August and September restricted to epilimnion.

Kellicottia bostoniensis. A deep-water species. May 28-July 17 restricted to the hypolimnion. O_2 depletion and related chemical changes forced species into the thermoclines during late July, August and September. Again found near bottom in late winter.

Polyarthra euryptera. Rather even distribution throughout epilimnion with distinct concentration zones in regions of rapid O_2 depletion.

Notes concerning the vertical distribution of other 14 species are included in the following section.

SEASONAL CHANGES IN ABUNDANCE

Seasonal changes in abundance of all Rotifera and of the five most numerous species are pictured in Figure 8. Total Rotifera and *Keratella cochlearis* are graphed on one scale and the other species on another, since their numbers were correspondingly lower. As will be shown in the following discussion, the 1937 and 1938 data are not completely identical, but both show clearly the major seasonal trends. For that reason it is felt that the 1933-34 winter series may be indicative of winter conditions in Douglas Lake.

Total Rotifera. Two definite maxima, one in late May and early June and one in September. Spring maximum apparently larger, although no samples available later than September 15, 1938. Two periods of minima, one in late summer and one during winter. In 1937, spring maximum also in late May. No September records available for that year.

Thus the abundance changes of the Rotifera take the form of a bimodal curve, typical of the annual production of plankton in many temperate lakes (Welch, 1935).

Keratella cochlearis. This species graphed on the same scale as total Rotifera in Figure 8. Evidently the dominant species. Maxima and minima mostly responsible for bimodal distributional curve of rotifer totals. Similar seasonal changes observed in 1937.

Conochilus unicornis. Abundant middle of May to middle of July, with definite maximum in early July; population small remainder of year. Maximum for 1937 in late June.

Kellicottia longispina. Two periods of abundance, one in spring corresponding to that of *Keratella cochlearis*, and one in late October and November. No indication of October maximum in 1937.

Kellicottia bostoniensis. Only one annual pulse, August and September, in both 1937 and 1938; population very small remainder of year.

Polyarthra euryptera. Present only during late May to middle August; always less than 20 per liter. In 1937 maximum population of 39 per liter on July 16.

It will be observed that for the preceding species the periods of maxima differ for most, and that some develop but one seasonal maximum, while others develop two.

The following are brief notes concerning seasonal changes in vertical distribution and in abundance of 14 other Douglas Lake plankton Rotifera. Throughout it should be understood that the expression *general distribution* signifies the occurrence of the species concerned at practically all of the depths sampled, where the number of individuals at each depth may vary. Similarity in the number of individuals at each depth is referred to as *uniform distribution*. Occasional individuals distributed at various depths will be referred to as *scattered*.

Ascomorpha ecaudis. Almost invariably restricted to upper 10 meters; scattered; number of individuals never exceeded 5 per liter; most frequent in September and October; absent from samples November into early May.

Asplanchna priodonta. Usually found in upper 10 meters; scattered; number of individuals never exceeded 13, usually 1 or 2; more frequent August into October; absent from samples late October into early May.

Collotheca mutabilis. Quite uniformly distributed from surface to bottom, with only occasional maxima near surface or in hypolimnion; number per liter usually less than 10, sometimes up to 33; no records in samples from November into early April; consistently present remainder of year with slightly higher numbers in series of June 29-30, 1938.

Filinia longiseta. During February into early May generally distributed; in summer and autumn scattered vertically; numbers not exceeding 74 per liter in winter and spring, and invariably less than 8 in summer and autumn; most frequent in February, April and May, with apparent tendency to congregate in deeper water.

Gastropus stylifer. During May and October generally distributed; restricted to epilimnion in summer; scattered vertically in September; number of individuals never exceeding 37 per liter; more frequent in May and in September; rare June into August, numbers never exceeding 8 per liter; absent October to April inclusive, 1933-34.

Keratella cochlearis f. *macracantha*. Scattered ver-

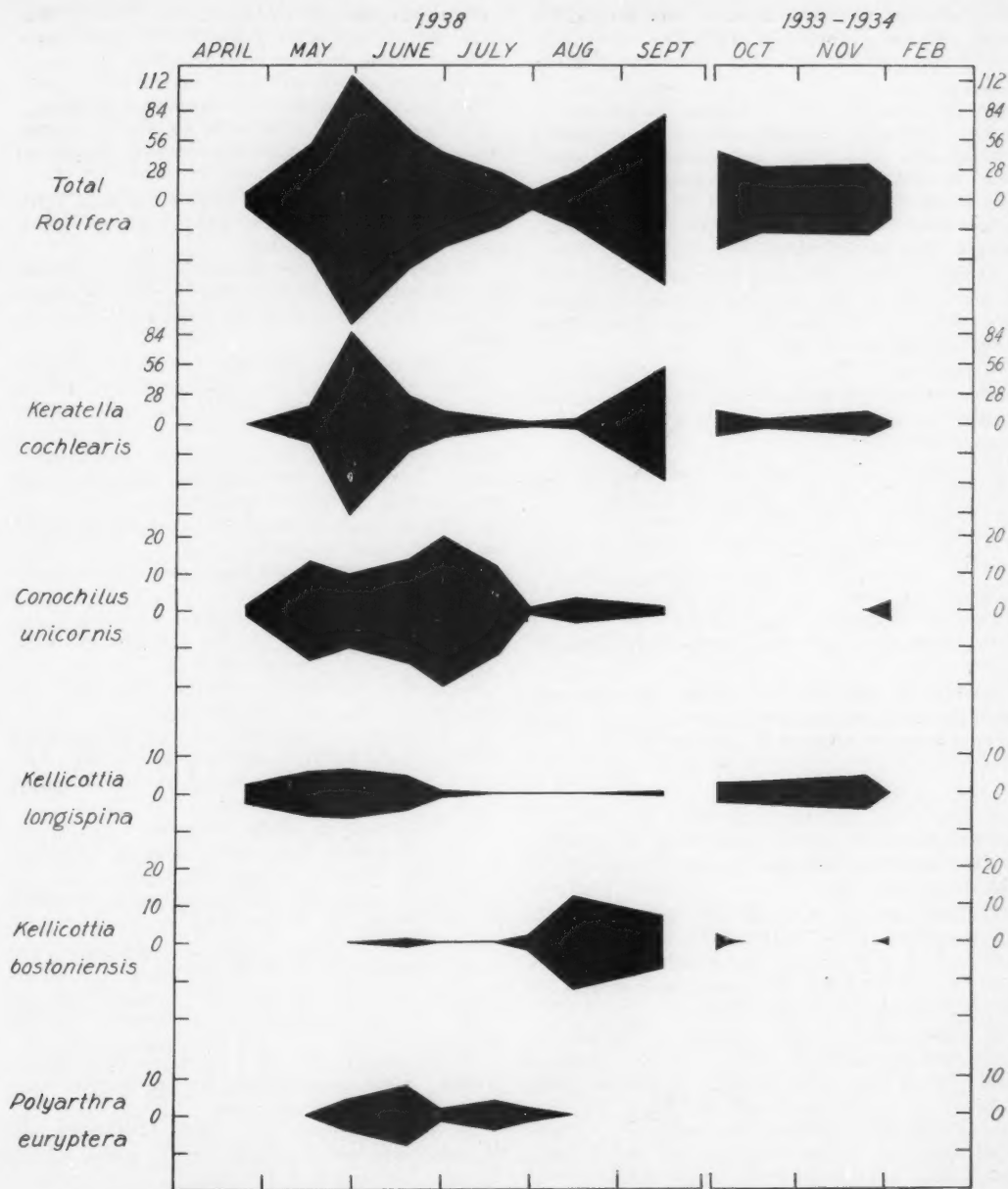


FIG. 8. Quantitative seasonal changes in certain Rotifera in Douglas Lake, April into September, 1938, and October into February, 1933-34. Figures record average number of individuals per liter of lake water for all depressions combined. Averages of less than 0.5 individuals per liter are not shown. Total Rotifera and *Keratella cochlearis* are plotted on a different scale than that used for the other four species.

tically; largest recorded number 44; usually less than 10 individuals per liter; scarce throughout year with little evidence of seasonal fluctuation.

Keratella cochlearis f. *robusta*. In August and September usually restricted to upper 14 meters, and there generally distributed; remainder of year de-

cidedly scattered vertically; maximum number 120, but usually less than 10 per liter; population increasing in August to maximum in September; remainder of year very scarce.

Keratella quadrata var. *divergens*. When present, usually in water deeper than 12 meters; much scat-

tered vertically; maximum number recorded 19, but usually less than 6 individuals per liter; absent from samples late October into May; scarce remainder of year.

Keratella quadrata var. *brevispina*. When present, scattered vertically; maximum number of individuals recorded 238; 1934 records indicate maximum under ice cover in April; population decreased rapidly, almost disappearing in June; absent from records July to November inclusive; in February population usually less than 10 individuals per liter.

Notholca striata. Scattered vertically; number individuals not exceeding 5 per liter; present in February, April and occasionally in May; absent from samples remainder of year.

Ploesoma spp. Scattered vertically; when present, number of individuals usually less than 5; maximum number recorded 18; absent from samples late October into May.

Polyarthra trigla. Usually scattered vertically, but generally distributed May and June; maximum number of individuals recorded 373; common May and June, and October into November; rather scarce remainder of year.

Pompholyx complanata. When present, scattered vertically; exceedingly rare, largest number 22 per liter; absent from samples November to June inclusive.

Trichocerca cylindrica. Scattered vertically; exceedingly rare; largest number of individuals 3 per liter; absent from samples October into June.

SUMMARY

1. This paper represents the first detailed comparative study of vertical distribution of plankton Rotifera in several submerged depressions within one wide-open lake basin.

2. Data herein presented are based upon 641 plankton samples, collected in the winter of 1933-34 and during the spring, summer and autumn of 1937 and 1938 in Douglas Lake, Michigan, together with accompanying physico-chemical data.

3. Confirmation of the existence of thermal depression individuality is drawn from the following facts: In the various depressions (a) thermal stratification was established on different dates; (b) thermoclines varied in thickness and positions; (c) complete autumnal overturning occurred on different dates; and, (d) bottom-water temperatures differed on corresponding dates.

4. Confirmation of the existence of chemical depression individuality is based upon the following facts: In the several depressions and on corresponding dates (a) the rate and extent of O_2 exhaustion was different; (b) the region of rapid O_2 decline differed in thickness and in depth; and (c) differences existed in free CO_2 and in pH distribution.

5. Proof of the existence of differences in rotifer distribution among depressions rests upon the following facts:

(a) Population concentration zones were established on different dates in the several depressions. They also disappeared on different dates.

(b) Depth positions of the concentration zones varied among depressions on corresponding dates.

(c) Concentration zones differed among depressions with respect to their approximate widths, on corresponding dates.

(d) Magnitude of concentration zones (i.e., number of individuals per liter) differed among depressions on corresponding dates.

(e) Late in the winter stagnation period, population concentration zones existed at different depth levels in the three depressions which received winter study.

(f) The preceding statements are based upon distributional patterns of total Rotifera and of species.

6. Rotifer distribution was found to be similar during both summer and winter stagnation periods, being characterized by population concentration zones. Distribution was generally uniform during both vernal and autumnal overturns.

7. Population concentration zones occurred in the regions of rapid O_2 decline.

8. Rotifera usually were absent from strata devoid of O_2 .

9. Numerical decrease was usually marked in the transition zone between the stratum with rapid O_2 decline and the stratum devoid of O_2 .

10. Rotifer distribution appeared to be closely related to O_2 , CO_2 , and pH changes.

11. Little or no distributional changes occurred within the thermoclines, save late in summer when, apparently, O_2 conditions forced the concentration zones within the thermoclines.

12. Differences in rotifer distribution among depressions appears to be related to chemical differences among depressions on corresponding dates.

13. By August 15, 1938, practically the entire rotifer population was confined to the upper 15 meters.

14. Seasonal changes in abundance of total Rotifera take the form of a bimodal curve, typical of the annual production of plankton in many temperate lakes.

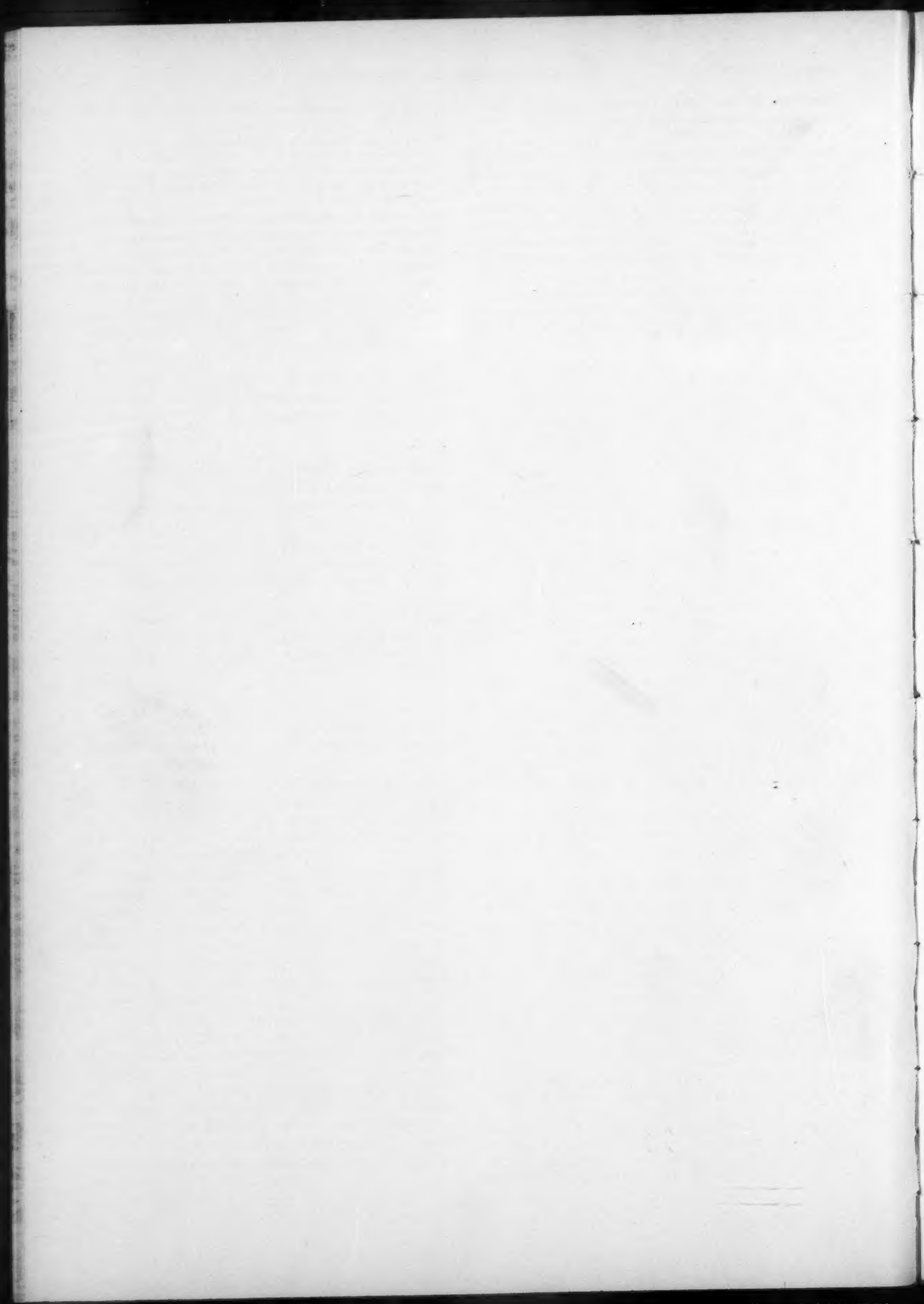
15. Periods of maxima and minima differ among species. Some species develop but one seasonal maximum, while others develop two.

16. Seasonal changes in vertical distribution and in abundance are discussed for 19 species of the Douglas Lake plankton Rotifera.

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LIMNOLOGICAL STUDIES IN CONNECTICUT
IV. THE MECHANISMS OF INTERMEDIARY METABOLISM
IN STRATIFIED LAKES

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	23
TEMPERATURE AS AN INDICATOR OF TURBULENCE.....	23
1.1.1., 1.1.2. The Data.....	23
1.2. Observed Variation of $\frac{\partial \theta}{\partial t}$ with z	25
1.3.1.-1.3.4. Determination of the Clinolimnetic Coefficient of Turbulence.....	25
1.4. Criterion of Validity	28
1.5.1., 1.5.2. Critique of McEwen's Theory.....	29
1.6.1., 1.6.2. Conditions in the Epilimnion.....	30
1.7. Effect of Solar Radiation on the Clinolimnion.....	30
1.8. Vertical Constancy of Turbulence in the Clinolimnion.....	30
1.9. Temporal Variation of the Coefficient of Turbulence.....	31
1.10.1.-1.10.4. Conditions in the Bathylimnion.....	31
1.11.1., 1.11.2. Role of Density Currents.....	34
1.12. Grote's Regional Modulus of Turbulence.....	36
1.13. Comparison with the Results of Previous Investigators.....	36
ALKALINITY AS AN INDICATOR OF WATER-MOVEMENTS AND OF THE METABOLIC CONDITION OF THE HYPOLIMNION.....	36
2.1. The Data.....	36
2.2.1., 2.2.2. The Form of the Alkalinity Curve.....	36
2.3.1.-2.3.3. The Rate of Change of Alkalinity with Time.....	38
2.4. Estimate of Bicarbonate Output from Unit Mud Surface.....	39
2.5.1., 2.5.2. Carbon Dioxide Anomaly.....	40
2.6.1.-2.6.3. Bases in Equilibrium with Bicarbonate.....	41
2.7. Comparison with the Results of Other Investigators.....	42
THE PHOSPHORUS CYCLE IN LINSLEY POND.....	43
3.1.1., 3.1.2. The Data.....	43
3.2.1., 3.2.2. Nature and Proportions of the Forms of Phosphorus Present in the Surface Water.....	44
3.3.1.-3.3.4. Total Phosphorus Estimated for the Entire Lake.....	45
3.4. Phases of Stagnation.....	46
3.5.1.-3.5.4. Vertical Distribution of Phosphorus.....	47
3.6.1., 3.6.2. Comparison with Other Lakes.....	51
3.7.1.-3.7.4. Relationship of Iron and Phosphorus.....	52
3.8.1.-3.8.3. Phosphorus and Nitrogen as Limiting Factors.....	54
3.9. Horizontal Currents as a General Factor in Limnetic Intermediary Metabolism.....	55
3.10.1.-3.10.4. The Phosphorus Cycle as a Specific Example of Intermediary Metabolism.....	56
SUMMARY	57
BIBLIOGRAPHY	58

THE MECHANISMS OF INTERMEDIARY METABOLISM IN STRATIFIED LAKES

INTRODUCTION

THE FUNDAMENTAL problem to be considered in the present paper is raised by the work of Juday and Birge (1931), who, unable to find clear evidence in a number of lakes of the depletion of phosphate in the epilimnion during summer stagnation, write "in some of the . . . lakes the quantity of soluble phosphate was maintained or was even increased somewhat during the growing season in spite of the fact that these bodies of water sustain a relatively large growth of phytoplankton." This observation suggests that our knowledge of the detailed movements of nutrients and other substances dissolved in the water of lakes is inadequate. A considerable body of information is available as to the total quantity of various important substances present in lakes. Observations on the oxygen deficit and various studies of the photosynthetic and katabolic activity of the plankton have given some information, often, however, of a very relative nature, as to the total metabolism of lakes. The intermediary aspect of metabolism, to continue the analogy with the individual organism, is extremely little known.

The method to be adopted in the present attempt to elucidate this problem may be briefly outlined in the following general terms. Before any biological activities can be considered, it is necessary to have an understanding of the purely physical movements of substances in a thermally stratified lake. The most easily treated type of disturbance causing transport of material is vertical turbulence, whereby conservative properties (insofar as they do not affect density) are transmitted through the water-mass according to laws of the same forms as those expressing the conduction of heat through a solid, but in which the coefficient of conduction is replaced by a virtual diffusion coefficient, the coefficient of turbulence or eddy-conductivity coefficient. Such vertical turbulence is the result of horizontal currents, generated by the wind. It is first necessary to examine the competence of turbulence to act as the agent producing observed effects, and insofar as this competence can be established, to estimate the value of the virtual diffusion coefficient involved. In certain cases it becomes apparent that vertical turbulent transport is inadequate to explain observed changes in properties. Knowing the distribution of the property in question, its rate of change, and the magnitude of the coefficient of turbulence, it is possible to estimate what part of the observed change is due to vertical turbulent mixing and what part to other causes. Such other causes are primarily the horizontal movements of water from the mud-water interface towards the middle of the lake, movements which, by generating vertical turbulence, are also indirectly responsible for the vertical exchanges. This procedure is the reverse of that usually adopted in oceanography but is probably a

far more convenient one for the study of small lakes than one founded primarily on direct observation of horizontal current systems. The first part of the paper, in which turbulence coefficients are evaluated, is based on a study of vertical series of temperatures. The second part in which residuals due to non-turbulent transport are obtained, is based primarily on a study of the bicarbonate content of a single lake, the concentration of this ion being regarded as conservative in the free water in the lake in question. In the third part the theory of water-movements evolved in the first two parts is applied qualitatively to elucidate the behavior of the phosphorus concentration, a highly non-conservative property of great biological interest. A number of related topics, of minor importance to the development of the general theory, but of considerable interest in themselves, are discussed in their appropriate places throughout the paper.

My best thanks are due to the Bache Fund of the National Academy of Sciences for generous financial support of my investigation, and to the Sheffield Fund of Yale University for a grant for special apparatus. I am also grateful to Dr. E. A. Birge and Dr. C. Juday for a table of weekly mean temperatures of Lake Mendota, which has been of the greatest value in the study of turbulence, to my former students and collaborators, Dr. G. A. Riley and Dr. E. S. Deevey, Jr., for invaluable help throughout the investigation, to Miss Anne Wollack and Mr. H. J. Turner who have expended much care in the analyses entrusted to them, and to the property holders on the shores of Linsley Pond, particularly Mr. C. S. Sargent and Mr. Alexander Day, who have taken an encouraging interest in the investigation. I should also like to express my debt to Dr. G. F. McEwen's paper "A Mathematical Theory of the Vertical Distribution of Temperature and Salinity in Water" (1929). The present contribution could never have been made without the stimulus supplied by McEwen's ingenious treatment, even though the conclusions that I have reached differ greatly from his. I am well aware that since my own studies have led me to theorize somewhat extensively, time may show that my speculations are unfounded. I can only hope that they will prove as great an impulse to some future investigator as McEwen's theory has been to me.

TEMPERATURE AS AN INDICATOR OF TURBULENCE

THE DATA

1.1.1. A series of fourteen sets of temperatures taken in the morning with a reversing thermometer in the center of Linsley Pond (Fig. 1), at one meter intervals, from the surface to a depth of 14 m., every week from the beginning of June to the end of August, 1937, and a similar series of eight



FIG. 1. Linsley Pond, from the northern shore.

sets taken in the center of Lake Quassapaug during July and August, 1938, constitute the new data to be analyzed. Of these, the Linsley series, owing to its greater completeness, is by far the more important. A description of both localities has been given by Riley (1939) in an earlier paper. Equally valuable in the initial stages of the investigation is the table of mean weekly temperatures in Lake Mendota prepared by Dr. E. A. Birge and used by McEwen (1929) in his analysis of the heating mechanism of lakes.

1.1.2. In all series of single temperature readings, irregular variations are observed, which are undoubtedly primarily due to the piling up of the epilimnion down wind and the consequent distortion of the isotherms. Such irregularities, while probably minimal in series from properly chosen stations, cannot be entirely avoided, and vitiate any attempt to consider the events relating to a single date. Accordingly, in the analysis of the Connecticut data, it has been found necessary to use only mean values for each depth, the mean value of the temperature, $\bar{\theta}$, at any depth z , being taken as the independent variable to which is related the mean rate of change of temperature with respect to time at that depth, $\left(\frac{\partial \bar{\theta}}{\partial t}\right)$.

To obtain the latter quantity, the data relating temperature to time have been fitted to a straight line, the slope of which is taken to be the rate required.

This does not imply that the rate of heating is constant at any depth, but merely that such a procedure is the simplest and probably only practicable method of obtaining a mean rate of change. In treating the data from the Connecticut lakes, the correlation coefficient of temperature and time was determined as a measure of the significance of the relationship observed. In one or two cases, the correlation is low enough to indicate that accidental disturbances are playing so great a part in determining the observed temperatures that at such depths the rate of change calculated from the regression equation is of little significance. In the case of the Mendota data, the rise in temperature throughout the heating period is, owing to the very large number of readings averaged in a single entry, very regular, and treatment relating to single weekly sets is possible in some cases, but there are irregularities in others that make valid conclusions difficult to draw, and for this reason and in order to compare the results with those from the Connecticut lakes, it has seemed advisable to treat the Mendota data from the middle of June to the middle of August in the same way as the Linsley and Quassapaug data were treated, except that calculations of the correlation coefficient were deemed unnecessary.

To avoid unnecessary zeros and to permit easy comparison with McEwen's results, the unit of depth is taken as one meter, of time as one month (considered as consisting of thirty days).

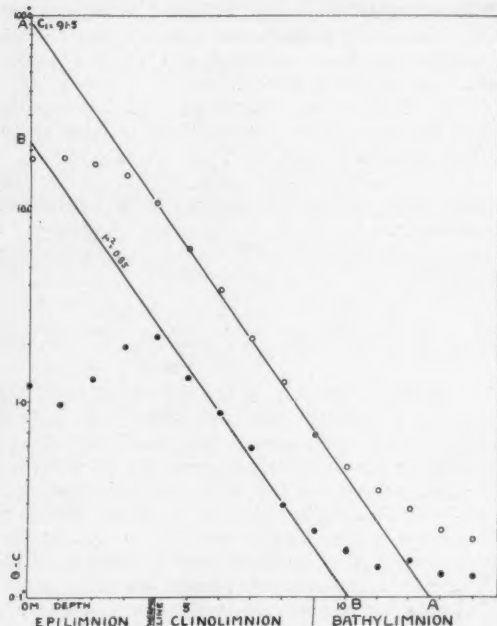


FIG. 2. Linsley Pond. Analysis of thermal conditions by procedure 1; mean data June-August, 1937. A-A', line of $(\theta - C) = C_1 e^{-az}$, $C = 6.82$, $C_1 = 91.5$, $a = 0.533$; observed values of temperature less 6.822 enclosed by open circles. B-B', lines of $\frac{\partial \theta}{\partial t} = \mu^2 C_1 a^2 e^{-az}$, where $\mu^2 = 0.85$; observed values of the rate of change of temperature with time entered as solid circles.

OBSERVED VARIATION OF $\frac{\partial \theta}{\partial t}$ WITH z

1.2. The solid circles in Figs. 2-7 indicate the observed values of the rate of change of temperature with respect to time, plotted, following McEwen, on the logarithmic axis of semilogarithmic paper, against depth. It will be immediately apparent that three regions can be distinguished in the lake differing in the nature of the variation of $\frac{\partial \theta}{\partial t}$ with depth.

(a) In the upper part of the lake, 0-4 m., in Linsley Pond, 0-6 m., in Lake Quassapaug, 0-9 m., in Lake Mendota, $\frac{\partial \theta}{\partial t}$ is relatively high and either may fall slightly with increasing depth, or, if late summer values are included in the calculation, may rise somewhat with depth. The region corresponds to the epilimnion.

(b) In the middle part of the lake, 4-9 m., in Linsley, 8-14 m., in Quassapaug, and 9-16 m., in Mendota, the value of $\frac{\partial \theta}{\partial t}$ falls exponentially with increasing depth, giving a distribution of points tending to lie on a straight line, at least in Mendota and Linsley, though more irregular in the case of

Quassapaug (vide 1.12). This region is here referred to as the *clinolimnion*, and is limited on its upper surface by the thermocline, treated as a plane; much of the thermocline region, as usually conceived, may be included in the *clinolimnion*.

(c) In the lower part of the lake, below 9 m., in Linsley, below 14 m. in Quassapaug, and below 16 m.

in Mendota, the values of $\frac{\partial \theta}{\partial t}$ are considerably higher than would be expected from extrapolation of the exponential fall in the *clinolimnion* and tend to become approximately constant at a value little if any lower than the lowest value at the bottom of the *clinolimnion*. This region is here termed the *bathylimnion*.¹ The hypolimnion is regarded in the present paper as comprising the *clinolimnion* and *bathylimnion*; the new terms are intended to be used only when problems of heating, turbulence and stability are under discussion.

DETERMINATION OF THE CLINOLIMNETIC COEFFICIENT OF TURBULENCE

1.3.1. Considering first the *clinolimnion* and assuming that the transmission of heat through this region is entirely by vertical turbulent mixing, and that density may be taken as constant and unity (Schmidt, 1925),

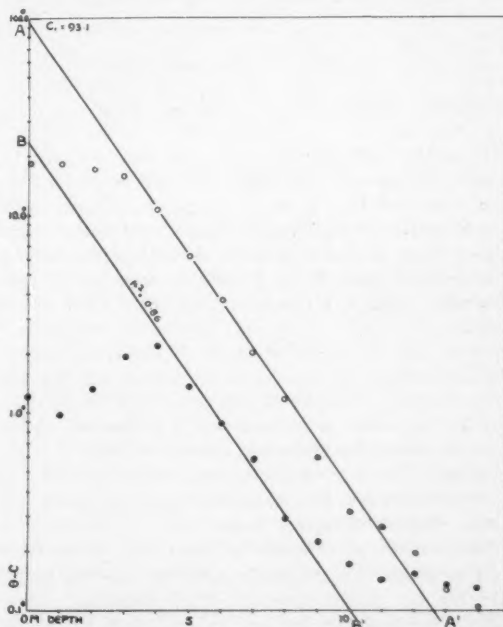


FIG. 3. Linsley Pond. Analysis of thermal conditions by procedure 2; mean data June-August, 1937. $C = 6.91$, $C_1 = 93.1$, $a = 0.540$, $\mu^2 = 0.86$. Otherwise as in Figure 2.

¹ It is not a permanent layer and must not be confused with the monimolimnion of Findenegg, which, however, may well be persistent development of the *bathylimnion*.

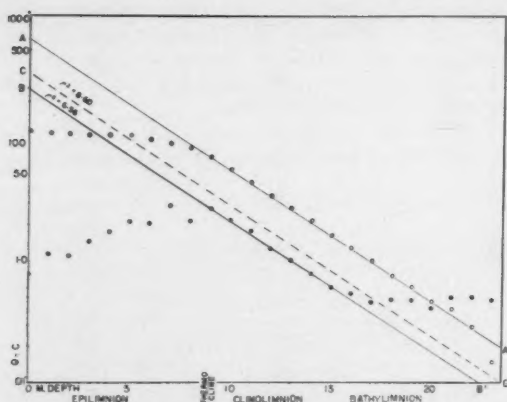


FIG. 4. Lake Mendota. Analysis of thermal conditions by procedure 2; mean data for the period from the third week in June to the second week in August. $C = 11.91$, $C_1 = 63.95$, $a = 0.246$, $\mu^2 = 6.55$. The broken line C-C' represents the calculated value for the rate of change in the hypolimnion if McEwen's procedure, using all points below 12 m., in the calculation of the coefficient of turbulence ($\mu^2 = 8.60$), is employed. Note that the observed values of $\frac{\partial \theta}{\partial t}$ are practically constant in the bathylimnion and show no tendency to fall on a line parallel with A-A' below 16 m.

$$\frac{\partial \theta}{\partial t} = \mu^2 \frac{\partial^2 \theta}{\partial z^2} \quad (1)$$

where μ^2 is the coefficient of turbulence, here considered as constant, having the dimensions of $\frac{L^2}{T}$, i.e.

(following McEwen), square meters per month. In oceanography the symbol A , in C.G.S. units, that is, cm^2 per second, is used; to permit easy comparison with McEwen's results and to avoid unnecessary zeros the former notation is more convenient throughout the greater part of the present section, but in paragraph 1.8.2. it is necessary to use C.G.S. units; both notations therefore have been used in tabulating results ($A = \mu^2 \times 3.858 \times 10^{-3}$). If the rate of change of temperature with time at a series of depths and the variation of temperature with depth in the same region be known, it is theoretically possible to obtain the coefficient by obtaining the second derivative directly. This, however, involves two mechanical differentiations of the temperature curve, which are undesirable, not merely because of the errors introduced in the operations, but because any errors in the original data are apt to produce inflection points in the temperature curve. Such inflection points cause artificial maxima and minima in the curve of the first derivative and changes of sign in the second. It is therefore preferable to use a more indirect treatment, in which the points of the temperature curve are fitted by a function, the second derivative of which is easily obtained. The fit of the observed points, however good, does not necessarily give any

information as to the mechanism of heating in the lake. It merely provides the best available method of obtaining a second derivative and is to be regarded as a quasi-fit (Riley 1939a).

1.3.2. McEwen has pointed out that it is possible to fit the hypolimnetic temperatures of lakes to an expression of the form

$$(\theta - C) = C_1 e^{-az} \quad (2)$$

where C , C_1 and a are constants to be determined empirically.

From (2)

$$\frac{\partial^2 \theta}{\partial z^2} = C_1 a^2 e^{-az} \quad (3)$$

hence

$$\mu^2 = \frac{\partial \theta}{\partial t} \cdot \frac{1}{C_1 a^2 e^{-az}} \quad (4)$$

The problem, therefore, is the determination of the constants in equation (2). According to the findings of the present investigation, this should only be permissible in the clinolimnion (procedure 1), but since the divergence from the fit in the bathylimnion is small and since the addition of more values to the rather meagre number available in the clinolimnion of the lakes under discussion appears to add greatly to the accuracy with which the fitting can be performed, all hypolimnetic values of θ , except the lowest, may be used in the process (procedure 2). The two procedures give essentially the same mean results in the clinolimnion; in working out an example in 1.3.4. procedure 1 has been used for the sake of brevity, but unless otherwise stated all values of the coefficient used in the discussion are those obtained by procedure 2.

1.3.3. Subtract the temperature at each depth, z_{n+1} , from that at unit depth above, z_n . Call the difference, considered as positive, $\Delta \theta$. For the permissible depths (procedure 1) or throughout the whole hypolimnion (procedure 2), construct a table:

z	θ	$\Delta \theta$	$\theta \cdot \Delta \theta$	$(\Delta \theta)^2$
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and add each column. It is now possible, by the least square method, to fit the observed values of θ and $\Delta \theta$ to a straight line of the form

$$\theta = C + b \Delta \theta \quad (5)$$

From equation (2), since for any value

$$\begin{aligned} \Delta \theta_n &= C_1 [e^{-na} - e^{-(n+1)a}] \\ &= C_1 e^{-na} (1 - e^{-a}) \\ &= (\theta_n - C) (1 - e^{-a}) \end{aligned}$$

$$\theta = C + \frac{\Delta \theta}{1 - e^{-a}} \quad (6)$$

This is of the same form as (5); C is the same in

$$\text{both equations and } e^{-a} = 1 - \frac{b}{C} \quad (7)$$

Having obtained C and a in this manner, the best value of C_1 may be obtained by summing the values of $(\theta - C)$ and dividing by the sum of the values of e^{-az} .

$$C_1 = \frac{\sum (\theta - C)}{\sum e^{-az}} \quad (8)$$

1.3.4. EXAMPLE (PROCEDURE 1)

Linsley Pond. June 1-August 31, 1937

z	$\bar{\theta}$	$\Delta\bar{\theta}$	$\bar{\theta}\Delta\bar{\theta}$	$(\Delta\bar{\theta})^2$
4	17.683	4.512	79.78	20.358
5	13.171	2.496	32.87	6.230
6	10.675	1.699	18.14	2.887
7	8.984	0.884	7.94	0.781
8	8.100	0.591	4.79	0.349
9	7.509	0.223	1.67	0.050
	$\Sigma = 66.122$	$\Sigma = 10.405$	$\Sigma = 145.20$	$\Sigma = 30.655$

Using the usual formulae for fitting by least squares:

$$p.C + b. \Sigma \Delta\bar{\theta} = \Sigma \bar{\theta}$$

$$\Sigma \Delta\bar{\theta}.C + b. \Sigma (\Delta\bar{\theta})^2 = \Sigma \bar{\theta}.\Delta\bar{\theta}$$

where p is the number of observations.

$$6C + 10.405b = 66.122$$

$$10.405C + 30.655b = 145.20$$

whence $C = 6.82$ and $b = 2.42$.

$$\text{From (7) } e^{-a} = 1 - \frac{2.42}{6.82} = 0.587$$

From Hayashi (1921)

$$a = 0.533$$

From (8) with observations at six levels

$$\Sigma_{z=4}^6 \bar{\theta} - 6 \times 6.82$$

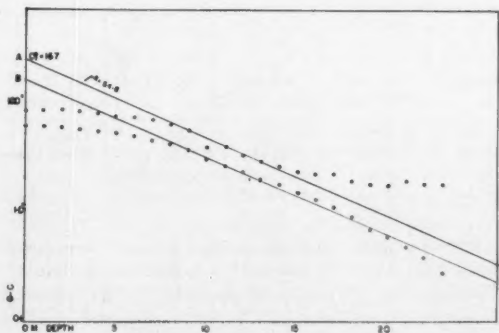
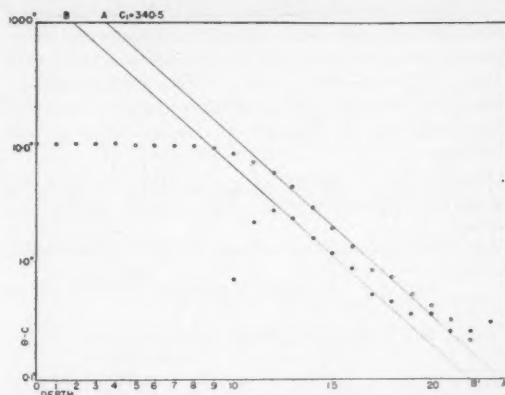
$$C_1 = \frac{\Sigma_{z=4}^6 e^{-az}}{\Sigma_{z=4}^6 e^{-az}}$$

From Hayashi, where $a = 0.533$.

	az	e^{-az}
4	2.12	0.119
5	2.67	0.070
6	3.20	0.041
7	3.73	0.024
8	4.26	0.014
9	4.79	0.008

$$0.276$$

$$C_1 = \frac{66.12 - 6 \times 6.82}{0.276} = 91.5$$

Knowing the constants C_1 and a , the coefficient of turbulence can now be calculated from equation (4)FIG. 5. Lake Mendota. Analysis of thermal conditions for the mean first week in June by procedure 2. $C = 10.83$, $C_1 = 15.85$, $a = 0.163$, $\mu^2 = 54.8$.FIG. 6. Lake Mendota. Analysis of thermal conditions for the mean fourth week in August by procedure 2. $C = 12.49$, $C_1 = 340.5$, $a = 0.345$, $\mu^2 = 4.86$.

for all clinolimnetic levels, the values obtained being set out in Table 1. In the same table values for the same region are set out using procedure 2. The results of the calculations by procedure 2 for Lake Mendota (mean) are set out in Table 2. Mean clinolimnetic values for the different weeks of the Mendota chart³ calculated by procedure 2, are given in Table 3. The results obtained by treatment of the inadequate data from Lake Quassapaug are discussed in 1.12; they raise certain special problems of interest but are too irregular to be of much significance in establishing general principles.

² Values of $\frac{\partial \theta}{\partial t}$ are obtained by the method of moments used by McEwen.

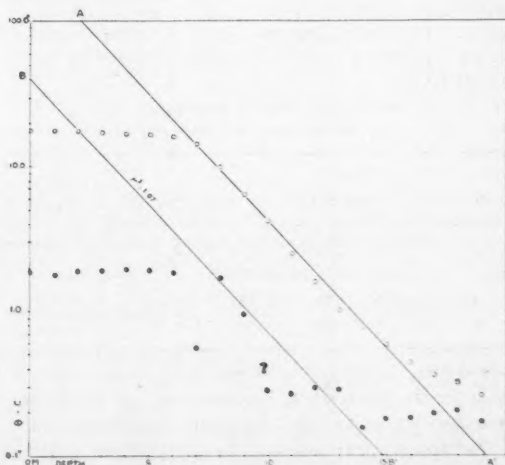


FIG. 7. Lake Quassapaug. Analysis of thermal conditions by procedure 2; mean data July-August, 1938. $C = 6.75$, $C_1 = 232$, $a = 0.404$, $\mu^2 = 1.07$. The ten meter value for $\frac{\partial \theta}{\partial t}$ has been rejected in calculating the coefficient of turbulence as the correlation of temperature with time at that level is insignificant ($r = 0.418$); this point is marked with a query (?).

In both Linsley and Quassapaug the values of A indicate that the observed coefficient is only about three times the coefficient of molecular heat transport (0.12×10^{-2} in C.G.S. units, Grote 1934); the turbulence coefficients in these lakes therefore are approximations, including effects due to molecular conduction.

TABLE 1. Analysis of thermal condition of the clinolimnion of Linsley Pond. (Mean values June-August, 1937.)

Depth m.	$\bar{\theta}$ °C	$\frac{\partial \theta}{\partial t}$ °C per month	μ^2 , m ² per month Proc. 1 C = 6.82 C ₁ = 91.5 a = 0.533	μ^2 , m ² per month Proc. 2 C = 6.91 C ₁ = 93.1 a = 0.540	Stability $\frac{d\sigma_g}{dz}$ grms per cm ³ per cm.	K = $A \cdot \frac{d\sigma_g}{dz}$
4.....	17.683	2.205	0.72	0.71	7.7x10 ⁻⁶	2.55x10 ⁻⁸
5.....	13.171	1.367	0.76	0.75	3.4x10 ⁻⁶	1.13x10 ⁻⁸
6.....	10.675	0.884	0.83	0.83	2.2x10 ⁻⁶	0.73x10 ⁻⁸
7.....	8.984	0.595	0.95	0.96	0.84x10 ⁻⁶	0.28x10 ⁻⁸
8.....	8.100	0.297	0.81	0.82	0.32x10 ⁻⁶	0.11x10 ⁻⁸
9.....	7.509	0.222	1.02	1.09	0.24x10 ⁻⁶	0.08x10 ⁻⁸
Mean μ^2 = 0.83, 0.86						
Mean A = 0.86 x 0.3852 x 10 ⁻² = 0.331 x 10 ⁻²						

TABLE 2. Analysis of thermal conditions in the clinolimnion of Lake Mendota (mean data for mid-June to mid-August).

Depth z, m.	$\bar{\theta}$ °C	$\frac{\partial \theta}{\partial t}$ °C per month	μ^2 , m ² per month Proc. 2 C = 11.91 C ₁ = 63.95 a = 0.246	Stability $\frac{d\sigma_g}{dz}$ grms. per cm ³ per cm.	K = $A \cdot \frac{d\sigma_g}{dz}$
9.....	18.83	2.65	6.27	2.6x10 ⁻⁶	6.56x10 ⁻⁸
10.....	17.43	2.17	6.54	2.2x10 ⁻⁶	5.55x10 ⁻⁸
11.....	16.21	1.80	6.96	1.8x10 ⁻⁶	4.54x10 ⁻⁸
12.....	15.24	1.27	6.31	1.22x10 ⁻⁶	3.08x10 ⁻⁸
13.....	14.58	1.01	6.41	0.85x10 ⁻⁶	2.14x10 ⁻⁸
14.....	13.99	0.79	6.42	0.73x10 ⁻⁶	1.84x10 ⁻⁸
15.....	13.49	0.62	6.36	0.52x10 ⁻⁶	1.31x10 ⁻⁸
16.....	13.14	0.54	7.15	0.37x10 ⁻⁶	0.94x10 ⁻⁸
Mean μ^2 = 6.55 m ² per month.					
Mean A = 2.52x10 ⁻² cm ² per sec.					

TABLE 3. Lake Mendota (data from Dr. E. A. Birge). Variation of coefficient of turbulence and stability in clinolimnion with time. McEwen's values of μ^2 are given for comparison.

Week	Range of clinolimnion	μ^2 , m ² per month	μ^2 , m ² per month McEwen	A, cm ² per second	Stability 12 m. grms per cm ³ per cm.	Stability 15 m. grms per cm ³ per cm.	K, 12 m.	K, 15 m.
1st June.....	9-15	54.8	84	21.1x10 ⁻²	0.38x10 ⁻⁶	0.26x10 ⁻⁶	8.02x10 ⁻⁸	5.49x10 ⁻⁸
2nd June.....	9-15	22.4	27.6	8.64x10 ⁻²	0.59x10 ⁻⁶	0.33x10 ⁻⁶	5.08x10 ⁻⁸	2.84x10 ⁻⁸
3rd June.....	9-16	8.02	15.2	3.09x10 ⁻²	0.85x10 ⁻⁶	0.43x10 ⁻⁶	2.63x10 ⁻⁸	1.33x10 ⁻⁸
4th June.....	9-15	9.26	11.1	3.57x10 ⁻²	0.78x10 ⁻⁶	0.46x10 ⁻⁶	2.79x10 ⁻⁸	1.64x10 ⁻⁸
1st July.....	9-15	13.80*	9.2	5.32x10 ⁻²	1.03x10 ⁻⁶	0.44x10 ⁻⁶	5.48x10 ⁻⁸	2.34x10 ⁻⁸
2nd July.....	9-16	8.27	11.4	3.19x10 ⁻²	1.09x10 ⁻⁶	0.64x10 ⁻⁶	3.48x10 ⁻⁸	2.04x10 ⁻⁸
3rd July.....	9-16	8.01	9.5	3.69x10 ⁻²	1.16x10 ⁻⁶	0.52x10 ⁻⁶	3.59x10 ⁻⁸	1.61x10 ⁻⁸
4th July.....	9-16	4.92	7.9	1.90x10 ⁻²	1.54x10 ⁻⁶	0.70x10 ⁻⁶	2.93x10 ⁻⁸	1.32x10 ⁻⁸
1st August.....	10-16?	3.60	4.5	1.39x10 ⁻²	1.68x10 ⁻⁶	0.71x10 ⁻⁶	2.04x10 ⁻⁸	0.99x10 ⁻⁸
2nd August.....	11-17	4.07	5.6	1.57x10 ⁻²	1.79x10 ⁻⁶	0.81x10 ⁻⁶	2.81x10 ⁻⁸	1.27x10 ⁻⁸
3rd August.....	12-18	3.67	6.4	1.41x10 ⁻²	2.02x10 ⁻⁶	0.91x10 ⁻⁶	2.84x10 ⁻⁸	1.28x10 ⁻⁸
4th August.....	12-18	4.86	6.2	1.87x10 ⁻²	2.40x10 ⁻⁶	0.83x10 ⁻⁶	4.99x10 ⁻⁸	1.55x10 ⁻⁸

* Poor fit on semilogarithmic paper.

CRITERION OF VALIDITY

1.4. In the above treatment it has been assumed that equation (2) gives a sufficiently accurate picture of the variation of temperature with depth in the hypolimnion to permit the use of equation (4), a convenient expression for the coefficient of turbulence. This seems to be justified by the accuracy with which the points representing $(\bar{\theta} - C)$ or in the case of figures 5-7, $(\theta - C)$ are fitted by the graphs of equation (2), plotted on semi-logarithmic paper. In applying equation (1) it is moreover necessary to assume that over a considerable range of depths the coefficient of turbulence is essentially constant. If this assumption is correct, the values of $\frac{\partial \theta}{\partial t}$, i.e.

$\mu^2 C_1 a^2 e^{-a z}$, should, in any region where turbulence is the sole mechanism of heat transport, not merely fall on a straight line, but on a straight line parallel to that representing equation (2), when plotted against depth on the same semi-logarithmic paper. Inspection of the graphs indicates that, when the best data are used, this is in fact the case in the

TABLE 4. Analysis of thermal conditions in the clinolimnion of Lake Quassapaug. Mean values July-August, 1938. (10 m. level rejected in computing μ^2 on account of the low value of r_{0t} .)

z, m.	$\bar{\theta}$ °C	$\frac{\partial \theta}{\partial t}$ °C per month	r_{0t}	μ^2
8.....	16.21	1.68	0.912	1.12
9.....	12.95	0.92	0.856	0.99
10.....	10.80	0.28	0.418	(0.42)
11.....	9.20	0.31	0.831	0.71
12.....	8.28	0.29	0.890	1.00
13.....	7.74	0.28	0.907	1.44
14.....	7.48	0.15	0.816	1.13
mean				1.07

clinolimnion. Such a criterion was pointed out by McEwen. When it is remembered that the two series of points are obtained in any given case by quite independent treatments, the parallelism shown, for instance in the clinolimnion in Figure 4, is very striking.

CRITIQUE OF MCEWEN'S THEORY

1.5.1. McEwen obtained his values of the coefficient of turbulence in Lake Mendota by summing the separate values of $\frac{\partial \theta}{\partial t}$ and dividing by the sum of the

separate values of $C\alpha^2 e^{-\alpha z}$, over the entire range of depths below 12 m., thus including those depths, between 16 m. and 23 m., here regarded as bathylinnetic,

where there is no trace of an exponential fall in $\frac{\partial \theta}{\partial t}$

with increasing depth. This procedure clearly violates the criterion of validity given in the preceding section, and leads to somewhat higher values of the coefficient of turbulence than those that have been obtained in the present work. In Figure 4 the dotted line represents the calculated rate of change of temperature with respect to time, due to turbulence, when McEwen's procedure is adopted. At all depths above 17 m. the water heats more slowly than would be expected, and it is necessary to explain the negative residual differences between the observed and cal-

culated values of $\frac{\partial \theta}{\partial t}$. These residuals form the

basis of the major part of McEwen's theory. It is supposed that cooling, largely by evaporation at the surface, reduces the temperature of discrete masses of water below the mean surface temperature, thus setting up differences of density. After a variable amount of cooling, the cooled elements are assumed to descend to levels appropriate to their new densities. This movement generates upward counter-currents of colder water and so causes a reduction in temperature at all those levels at which residuals are observed. The frequency of different classes of density difference is assumed to follow the normal probability distribution, and an elaborate expression is given, based on that assumption, to which the vertical series of residuals can be fitted. The theory is apparently accepted without comment by Grote (1936), but has been criticized by Behrens (1937) on general grounds. McEwen's choice of 12 m. as the limit beyond which the convection currents are undetectable, and in consequence as the limit below which no significant residuals due to the cold upward stream occur, appears to be quite arbitrary. Examination of the mean Mendota graph indicates that the events at 12 m. are essentially of the same kind as the events at 9 m.; inclusion of all depths up to nine meters, in estimating the coefficient of turbulence, would, however, lower the residuals considerably. Conversely, if the 9 m. level be excluded, so should all depths down to 15 m. be excluded. Moreover, below 16 m. the criterion for the validity of the

assumption of a constant value of the coefficient of turbulence, necessary for the application of McEwen's theory, does not hold; if these depths are rejected, in line with the point of view of the present paper, there are no residuals to form the basis of McEwen's theory.

1.5.2. As the basis of a further examination of the theory in so far as it is founded on the existence of residuals of the kind discussed in the preceding

paragraph, three hypotheses as to the values of $\frac{\partial \theta}{\partial t}$ in the bathylinnion may be offered.

(a) The apparent constancy of $\frac{\partial \theta}{\partial t}$ in Lake Men-

dota below 16 m. is due to observational error. This appears to be McEwen's position, being implied in his use of a mean value of the coefficient of turbulence. But since the apparent constancy is more clearly marked in the mean curve than in individual curves for separate weeks, such an assumption may be rejected, particularly when it is remembered that several hundred observations are represented by each of

the points representing $\frac{\partial \theta}{\partial t}$ in Figure 4. The fact

that similar phenomena occur in both the Connecticut lakes studied would also appear to exclude the hypothesis.

(b) A cooling mechanism exists through the whole vertical extent of the lake, becoming less and less effective with increasing depth. Such a cooling mechanism could only be the one suggested by McEwen. On the basis of this hypothesis McEwen's theory would be valid, his application of the theory to Lake Mendota invalid. The hypothesis indeed introduces an element of uncertainty into any application. An approximation to the coefficient of turbulence could

be obtained from the values of $\frac{\partial \theta}{\partial t}$ and $C\alpha^2 e^{-\alpha z}$ for

the greatest depth available, but there would be no way of telling how much the very large value (in the case of the mean Mendota data of Figure 4, at 23 m. the value would be $\mu^2 = 35.4$) and with it the estimates of the residuals, fell short of the true values. On the basis of this hypothesis the marked

exponential form of the fall of $\frac{\partial \theta}{\partial t}$ in the clinolim-

nion must be regarded as an accidental departure from a more complex type of distribution, and the criterion of validity of 1.4. is meaningless.

(c) Turbulence changes in the bathylinnion (1.10.1) or some other heating mechanism (1.10-1.11.) exists in this region. All bathylinnetic estimates of the coefficient of turbulence are therefore irrelevant in calculating the theoretical estimate of heating in the clinolimnion. The exponential fall in the latter region may therefore be taken as satisfying the criterion of validity, indicating that in the region in question only heat transport by vertical turbulence

with an essentially constant value for the coefficient is taking place. This is the position of the present paper. The first hypothesis (a) clearly cannot be reconciled with the facts. The second (b) though logically consistent is very complex; and though not in conflict with the observational data, receives no support from them. In the face of the third (c), much simpler hypothesis, it must be regarded as untenable, falling to the razor of William of Occam, with the whole theory of convectional cooling of the hypolimnion.

CONDITIONS IN THE EPIMLIMNION

1.6.1. The method given in 1.3.2. for the determination of the coefficient of turbulence is only applicable to the clinolimnion. McEwen attempted to apply a modification of the method to the epilimnion, but his procedure does not appear to be valid. Since in the temperature curves of practically all stratified lakes there is a well-marked inflection point defining the thermocline, there is clearly a region in the

epilimnion where $\frac{\partial^2 \theta}{\partial z^2}$ is negative, and where uni-

form turbulence produces a fall in temperature. McEwen's treatment on the other hand assumes a second exponential temperature curve set above that in the hypolimnion and entirely unlike the conditions actually found in any lake. All that can be said of the epilimnion is that the conditions are complex and that turbulence is undoubtedly high. A method for relative estimation of its magnitude in a series of lakes is given by Grote (1934) and is discussed in 1.12; no absolute estimate seems at present possible.

1.6.2. Although McEwen's theory is here regarded as definitely inapplicable to the hypolimnion, the possibility of its application to the extreme superficial layers of a lake, layers in which a very small thermal gradient is developed, must not be forgotten, in case some method be devised that would permit a detailed treatment of the thermal phenomena of the epilimnion. This possibility is suggested by an experiment performed by McEwen, in a concrete tank five feet deep, with a fall in temperature at midday from 26.74° C. at the surface to 25.10° C. at the bottom. Analysis of the rate of change of temperature with time during the day in this tank suggested that the convectional system postulated played a part in the heat exchange of the different water-layers. It must, however, be pointed out that in McEwen's treatment of events in the tank, it has been assumed, presumably correctly, that the water was free from turbulence, whereas it is clear that the epilimnion of a lake would be highly turbulent. The chief difficulty in applying the results of the experiment to the upper layers of a lake with a thermal gradient comparable to that in the tank lies in conceiving of the uninterrupted descent of discrete masses of water, through a layer as highly disturbed as the upper few meters of a lake, let alone of the open ocean, for the treatment of which the theory was originally elaborated. No information as to the size of the supposed discrete

masses is given, save that they are of more than molecular dimensions.

EFFECT OF SOLAR RADIATION ON THE CLINOLIMNION

1.7. It has seemed desirable to estimate, from the data of Birge and Juday (1929), the rate of heating due to solar radiation at and below 9 m. in Lake Mendota, though it is well known from the classical work of these authors, that such heating is very small. Using a mean value for radiation penetrating the lake surface, of 15,825 cal. per cm.² per month for the period mid-June to mid-August, and a percentile transmission of 45 (mean sun), 4.55 cal. per cm.² reach the 9 m. level per month, and being absorbed at this level at the rate of 2.5 cal. per cm.² per meter, cause a rise in temperature of 0.025° C.

per month. Since the observed value of $\frac{\partial \theta}{\partial t}$ at this

level is 2.65° C. per month, it is clear that an error of about one per cent is introduced by neglecting direct heating by radiation; at all succeeding levels the error will be less. The mean value of the coefficient of turbulence computed by procedure (2) for the whole clinolimnion is 6.54 if solar radiation be taken into account, and 6.55 if it be not; such a difference is insignificant.

VERTICAL CONSTANCY OF TURBULENCE IN THE CLINOLIMNION

1.8. Given constant mixing forces, the value of the coefficient of vertical turbulence is inversely proportional to the vertical stability. Yoshimura (1936, 1938) who has studied the coefficient of turbulence in Japanese lakes, but has so far not published his detailed conclusions, believes that this coefficient has a minimum value in the thermocline and increases in the deeper water of the lake. Such a belief is natural in view of the relationship just stated. A similar position is adopted by Grote (1934) on purely theoretical grounds. McEwen on the other hand makes no comment on his assumption of a uniform coefficient throughout the hypolimnion in spite of manifest changes in stability. Consideration of either the values derived from the mean Mendota, or from the Linsley data, or from any of the individual weekly series from the former lake, shows very definitely that the stability changes greatly with depth throughout the vertical extent of the clinolimnion, in which region the coefficient of turbulence is essentially constant. Putting the coefficient into C.G.S. units we can write, since A is proportional to the reciprocal of the stability,

$$A = K \cdot \frac{dz}{d\sigma_0}$$

or

$$K = \frac{d\sigma_0}{dz} \cdot A \dots \dots \dots (9)$$

K may be taken as a measure of the mixing forces producing turbulent exchange, and is a function of

the horizontal current velocity and the vertical gradient of such velocities. Assuming that the criterion of validity is satisfied, K is clearly proportional to the stability throughout the clinolimnion. On this assumption values have been computed by converting μ^2 to C.G.S. units (A) and multiplying by the stabilities throughout the clinolimnion. In the case of Mendota the values of stability were determined by mechanical differentiation of a density curve based on temperature alone. In the case of Linsley Pond, the chemical component of stability has been allowed for approximately, on the basis of an increase in density of 0.000018 per milligram per litre HCO_3 .³ The generalization that the coefficient of turbulence is minimal in the more stable layers is clearly erroneous insofar as the clinolimnion, defined by the condition of validity, is concerned. Moreover, if, as seems probable, the coefficient is essentially constant (1.10.3.) throughout the whole hypolimnion, the generalization is essentially false for all depths below the thermocline. The problem raised in this paragraph can only be discussed in terms of the horizontal currents which produce turbulence. The existence of such currents is implicit in all discussions of the turbulence problem, and in the second part of the present paper their implied existence is used to explain the chemical changes in the free water of the hypolimnion. Such currents certainly have velocities varying with depth. It is probable that important information as to their variation in velocity can be obtained from the constancy of the coefficient of turbulence with decreasing stability and decreasing mixing forces.

TEMPORAL VARIATION OF THE COEFFICIENT OF TURBULENCE

1.9. In marked contrast to the constancy of the mean values of the coefficient of turbulence in the clinolimnion with decreasing stability and increasing depth, there is a very marked decline in the value of the coefficient at all levels with increasing stability as the season advances (Table 3). In Figure 8 the

individual values of $\mu^2 = \frac{\partial \theta}{\partial t} \cdot \frac{1}{C_1 a^2 e^{-az}}$, at 12 and 15 m., are plotted against the reciprocal of the stability for all the weeks from the first in June to the last in August. The theoretically preferable mean values of the coefficient have not been used, to avoid overemphasis of the accuracy of the mean. The two depths were chosen as the highest and lowest that can be regarded as clinolimnetic throughout the entire period. In the same diagram the individual mean (mid-June to mid-August) values for the clinolimnion (Table 2) are indicated by the solid circles, which form an essentially horizontal line across the graph.

³ This figure is based on determinations with a 50 cc. picnometer on 13 m. filtered water taken on June 13, 1939, and having an alkalinity of 63.1 mgrms. per litre. Surface water of June 23, having an alkalinity of 58.6 mgrms. per litre gave a value of 0.0000014 per mgrm. HCO_3 in excess of distilled water, at 25.0°. The higher value of the 13 m. water is probably due to differential accumulation of other substances (organic matter, silicate, etc.); since the correction is applied to hypolimnetic water, this higher value has been used.

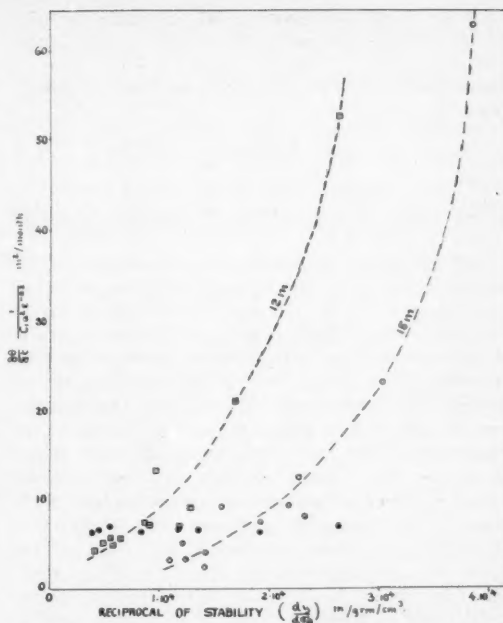


FIG. 8. Lake Mendota. The relationship between the value of $\frac{\partial \theta}{\partial t} \cdot \frac{1}{C_1 a^2 e^{-az}}$ and the reciprocal of stability at 12 m. (open squares) and 15 m. (open circles) for the various weekly mean temperatures for the period June-August, and between the same quantities at each depth between 9 and 16 m. (solid circles) for the mid-June to mid-August mean data.

The broken curves, which are fitted by eye and intended primarily to aid in the study of the diagram, would be straight lines if the mixing forces were constant throughout the period considered. Their form indicates that actually the mixing forces decline considerably during the progress of stratification. This is also apparent from Table 3, but after the middle of June the change is irregular, small, and perhaps insignificant.

CONDITIONS IN THE BATHYLIMNION

1.10.1. In the bathylimnion, the criterion of validity of 1.4. is no longer satisfied. In the mean Mendota graph (Figure 4) it is apparent that the rate of change of temperature with respect to time is essentially constant throughout the region. Two hypotheses have to be considered in the treatment of the region; the first is that turbulence is variable in the bathylimnion, the second that turbulence remains constant throughout practically the whole of the hypolimnion, but that other heating mechanisms play a part in the deeper water. A third hypothesis, that turbulence varies and that other mechanisms exist, is too complex to be considered unless the first two fail. Two equations, other than (1), give expressions for the coefficient of turbulence at any point. When turbulence is variable, the more general form of (1) is (Schmidt 1925)

$$\frac{\partial \theta}{\partial t} = \frac{d(\mu^2)}{dz} \cdot \frac{\partial \theta}{\partial z} + \mu^2 \frac{\partial^2 \theta}{\partial z^2} \quad (10)$$

while in all cases the transport equation (Schmidt 1925)

$$\frac{d\Theta}{dt} = -\mu^2 \frac{\partial \theta}{\partial z} \quad (11)$$

is valid, where $\frac{d\Theta}{dt}$ is the rate of total heat transport

across unit area. Equation (11), on account of its simplicity, has been used by many workers, including some interested in the transport of biologically active materials (e.g. Redfield, Smith, and Ketchum, 1937). It suffers, however, from the very grave defect that the value of μ^2 at any level is dependent on all exchanges, due to turbulence or to any other mechanism, beyond that level. Although, as will be shown in paragraph 1.10.3., this equation is of great utility in solving the present problem, its use naturally brings up the question of heating mechanisms other than vertical turbulent exchange. It is therefore appropriate to investigate briefly the value of the much more intractable second order differential equation (10) on the basis of the mean Mendota figures, which, here as elsewhere, may be used as a norm to which conditions in other lakes may be referred.

1.10.2. Assuming that the temperature curve may be expressed by equation (2), at least almost to the bottom of the lake, and that the rate of change of temperature with respect to time is constant throughout the bathylimnion, i.e.,

$$\frac{\partial \theta}{\partial t} = b = \text{constant}$$

equation (10) takes the form

$$b = \mu^2 C_{1a}^2 e^{-az} - \frac{d\mu^2}{dz} C_{1a} e^{-az} \quad (12)$$

$$\text{Now putting } \frac{b}{C_{1a}} = k$$

and writing in operational form, this becomes

$$(D - a) \mu^2 = -k e^{az}$$

The solution of this is

$$\mu^2 = (Q - kz) e^{az} \quad (13)$$

This belongs to a class of solutions⁴ of (10) which has no physical meaning below a certain depth, the turbulence coefficient decreasing more and more rapidly, and becoming zero at $z = \frac{Q}{k}$. Now if it be

assumed that the variation of the coefficient is continuous across the boundary of the clinolimnion and

⁴ Putting $\frac{\partial \theta}{\partial t} = \text{constant}$, it is easy to see, by differentiating (10) with respect to depth, that, provided the temperature curve has negative first and third derivatives with respect to depth, which is presumably the normal condition in holomictic lakes, the coefficient of turbulence can vary, given suitable forms of $\theta = f(z)$, so that its first and second derivatives with respect to depth are both negative, or both positive, or the first is positive, the second negative; the case in which the first is negative, the second positive is excluded. Equation (12) belongs to the first of these classes.

bathylimnion, the constant of integration Q can be determined by putting μ^2 equal to the clinolimnetic value when the depth z is taken as the depth of the boundary. In this way it can be shown, using the mean Mendota data, that the coefficient of turbulence would assume meaningless negative values below 20.2 m. The hypothesis of purely turbulent heating in the bathylimnion therefore does not seem a fruitful one, though it may be urged that the impasse just reached is implicit in the assumptions rather than in the observational data.

1.10.3. Turning now to equation (11), the values of the coefficient may first be computed by summing the heat income per unit of time and area, of each unit layer of a column in the deepest part of the lake. This quantity, when divided by the rate of change of temperature with depth, the minus sign being omitted, gives a set of apparent values for the coefficient of turbulence. This has been done for the mean Mendota

data in Table 5, $\frac{\partial \theta}{\partial z}$ being taken as $-C_{1a} e^{-az}$. In

Table 6 the same procedure has been applied to the Linsley data, but in this case, as the fit of the temperature curve to equation (2) is far from perfect, values have been calculated both from the expression

$-C_{1a} e^{-az}$ and from values of $\frac{\partial \theta}{\partial z}$ obtained directly

from the temperature curve by means of the Richards-Roope tangentmeter (Richards and Roope, 1930). In the case of the Mendota data the depth of the lake was taken as 24 m., the figure used by Birge (1916a), and the rate of change of temperature at 24 m. was taken to be the bathylimnetic mean of 0.476° C. per month. In the case of Linsley Pond the whole 13-14.8 m. stratum was taken to heat at the rate observed at 14 m. Uncertainty as to what maximum depth should be used in the case of Mendota does not invalidate the final treatment of the data. It will be observed that at the top of the clinolimnion, the values of the coefficient of turbulence approach those obtained from the simple second order equation (1), but that with increasing depth they diverge from the clinolimnetic values accepted in Tables 2 and 3. Since, at least in Figure 4, the criterion of validity is so clearly satisfied, it is certain that these increasing apparent values are

erroneous. If now, at each level, the rate $\frac{d\theta'}{dt}$ at

which heat is received through unit area in unit time be calculated from the clinolimnetic coefficient previously obtained, i.e. 6.55 m²/month in Mendota, 0.86 m²/month in Linsley, it will be observed that there is a well defined tendency for the difference between these calculated rates of heat income and the observed rates to be constant, as is indeed implicit on the exponential arrangement. In Mendota this is very marked in the whole clinolimnion, the mean difference being 184.1 cal. per cm² per month. In Linsley Pond there is great divergence between the two methods of calculation at 4 and 5 m., but from

6 to 9 m. fair constancy obtains, with mean values of 62.4 cal. per cm^2 per month if the derivative be calculated and 58.9 cal. per cm^2 per month if it be obtained by mechanical differentiation. The most reasonable conclusion to be drawn is that heat is entering the bathylinnion by non-turbulent mechanisms at a

rate of 184 cal. per cm^2 per month in the case of Lake Mendota and of about 60 cal. per cm^2 per month in the case of Linsley. Now let it be assumed that the coefficient of turbulence is constant throughout the entire hypolimnion. Using the values of $\mu^2 C_1 a^2 e^{-\mu z}$ for each bathylinnetic level, it is possible

TABLE 5. Computation of the mean rate of heating not due to vertical turbulent mixing, below one square centimeter over the deepest water (taken as 24 m.) of Lake Mendota (mid-June to mid-August), as the mean of the clinolimnetic residuals (mean of column 6) or as the sum of bathylinnetic residuals on the assumption of constant hypolimnetic turbulence (sum of column 9).

(1) Depth z m	(2) $\frac{d\theta}{dz}$ °C per m. or cal. per per m^3 per $\text{m} \times 10^{-6}$	(3) $\frac{d\theta}{dt}$ cal. per cm^2 per month or month $\times 10^{-4}$	(4) Apparent coefficient of turbulence $\frac{d\theta}{dz}$ $\frac{d\theta}{dt}$ m^2 per month	(5) $\frac{d\theta'}{dt}$ $= \mu^2 C_1 a^2 e^{-\mu z}$ where $\mu^2 = 6.55$ cal. per cm^2 per month	(6) Residual heating $\frac{d\theta}{dt} - \frac{d\theta'}{dt}$ cal. per cm^2 per month	(7) $\mu^2 C_1 a^2 e^{-\mu z}$ assuming constant turbulence $\mu^2 = 6.55$ °C per month	(8) $\frac{\partial \theta_{nt}}{\partial t} = \frac{\partial \theta}{\partial t} - \frac{\partial \theta'}{\partial t}$ °C per month	(9) Rate of non- turbulent heating for unit layer below depth z cal. per cm^2 per m. per month
9.....	-1.72	1309.9	7.61	1126.0	183.9			
10.....	-1.34	1069.0	7.96	880.0	189.0			
11.....	-1.05	870.8	8.29	688.0	182.8			
12.....	-0.822	717.2	8.73	538.0	179.2			
13.....	-0.642	602.9	9.39	420.3	182.6			
14.....	-0.500	512.7	10.25	327.5	185.2			
15.....	-0.393	442.5	11.26	256.2	186.3			
16.....	-0.307	384.7	12.52	201.1	183.6	0.495	0.045	6.1
					mean 184.1			
17.....	-0.241	334.5	13.88			0.388	0.077	13.2
18.....	-0.187	286.8	15.33			0.302	0.187	21.5
19.....	-0.146	238.4	16.33			0.236	0.243	23.4
20.....	-0.115	193.9	16.86			0.185	0.225	29.7
21.....	-0.0897	147.3	16.43			0.145	0.368	38.0
22.....	-0.0708	96.3	13.60			0.114	0.392	38.7
23.....	—	—	—			0.089	0.383	39.6
(24).....	—	—	—			0.068	0.408	
								Sum 210.2

TABLE 6. Computation of mean non-turbulent heating in the bathylinnion of Linsley Pond.

(1) Depth m.	(2) $\frac{d\theta}{dz}$ °C per m	(3) From graph $\frac{d\theta}{dz}$ °C per m	(4) cal. per cm^2 per month	(5) $\frac{d\theta}{dt}$ cal. per cm^2 per month	(6) $\frac{d\theta'}{dt}$ cal. per cm^2 per month	(7) $\mu^2 C_1 a^2 e^{-\mu z}$ assum- ing constant tur- bulence °C per mo.	(8) $\frac{\partial \theta_{nt}}{\partial t} = \frac{\partial \theta}{\partial t} - \frac{\partial \theta'}{\partial t}$ °C per month	(9) non-turbulent rate of heating of unit layer below depth, cal. per cm^2 per m. per month
4	5.79	4.9	447.2	-29.8	50.4			
5	3.47	4.2	334.8	52.8	- 5.2			
6	1.966	1.93	232.2	72.9	75.8			
7	1.145	1.30	158.3	59.9	53.1			
8	0.609	0.88	113.7	59.5	42.4			
9	0.377	0.28	87.7	57.2	64.4	0.175	-0.047	6.1
	mean (6-9m)		62.4	58.9				
10						0.100	0.075	7.9
11						0.058	0.083	10.1
12						0.034	0.120	11.7
13						0.018	0.114	11.6
14						0.012	0.117	21.1
								(to 14.8 m)
								Sum 68.5

to calculate the rate of turbulent and non-turbulent⁵

$\left(\frac{\partial \theta_{nt}}{\partial t}\right)$ change of temperature of each level. The

total rate of non-turbulent income of heat into the bathylinnion can be calculated by summing the mean non-turbulent rate of change for each layer, and is estimated as 210.1 cal. per cm^2 per month in the case of Mendota, 68.5 cal. per cm^2 per month in the case of Linsley Pond. These figures indicate that while the estimates of the turbulent heating based on assuming the clinolimnetic coefficient to hold are perhaps a little too high, the coefficient of turbulence cannot be very different in the bathylinnion from what it is in the clinolimnion. Similar phenomena also occur in Lake Quassapaug. The values of the residuals obtained when the heating below any clinolimnetic level as calculated is subtracted from the value observed are fairly constant between 11 and 14 m., the mean value being 72.0 cal. per cm^2 per month; the values derived from the 8-10 m. levels are low, probably due to the unreliability of the data. The value calculated on the assumption of constant turbulence

⁵ Turbulent and non-turbulent here refer only to vertical turbulent exchanges.

in the whole hypolimnion is 76.8 cal. per cm² per month; considering the nature of the data the agreement is remarkable. It is important to note that the quantity of heat brought into the bathylinnion of this lake by mechanisms other than vertical turbulent mixing is of the same order of magnitude as in Linsley Pond, in spite of the lesser depth of the latter. Per unit depth or volume, therefore, the non-turbulent mechanism is best developed in Mendota, least in Quassapaug.

1.10.4. In the use of equation (11) in the preceding paragraph, it has been assumed that the whole of the heat taken up by a column of water, below any given horizontal surface, has entered through the area of that surface defining the top of the column. It has been shown that, considering a column in the deepest part of the lake, heat enters the base of the column, in the bathylinnion, by some agency other than vertical turbulent transport. In the clinolimnion, since the criterion of validity of 1.4 is satisfied by the distribution of rates of change, the effect of such an agency is negligible. It remains to be considered whether this heat has been transmitted by vertical turbulent mixing, through some area of a horizontal plane at depth z , lying above the top of the bathylinnion, lateral to the deepest part of the lake, in relatively shallow water. Such a transmission of heat would imply that some of the heat passing through the area a_1 arrives, after lateral displacement, in more centrally situated deep water. This type of transmission is assumed in the calculation of heat budgets by the Wojeikoff-Birge method, while the budget (Θ) used in the preceding paragraph is essentially a Forelian budget. Birge (1916) has shown conclusively that the Forelian mode of estimation is erroneous, in that it leads to impossibly high figures in certain cases. The rate of change of the heat budget below a given level can be calculated not merely on a Forelian basis, as in the last paragraph,

but on a Birgean basis ($\frac{d\Theta_b}{dt}$) also. This is done

by multiplying the mean rate of change for any unit layer by the volume of the layer, summing upwards to any desired depth z , and dividing by a_1 , the area at that depth. This gives a rate of change based on the assumption that all the heat present in the lake below any level z has been evenly distributed over the area a_1 in its passage through that level; some form of lateral heat transmission is necessarily assumed. It is now possible, by the use of equation (11), to determine anew the coefficient of turbulence in the clinolimnion. The results of such a procedure for Linsley Pond are set out in Table 7, together with the apparent values of the coefficient obtained in the preceding paragraph on a Forelian basis, and the

values of $\frac{\partial \Theta}{\partial t} \cdot \frac{1}{C_1 a_1 e^{-az}}$ obtained by procedure

(2) in Table 1. It will be observed, that though the estimates in the second column show an increasing trend, this is much less marked than is the trend

TABLE 7. Estimates of Coefficient of Turbulence. Figures in parentheses obtained by mechanical differentiation.

	$\frac{d\Theta}{dt} \cdot \frac{\partial z}{\partial \bar{h}}$	$\frac{d\Theta_b}{dt} \cdot \frac{\partial z}{\partial \bar{h}}$	$\frac{\partial \Theta}{\partial t} \cdot \frac{1}{C_1 a_1 e^{-az}}$
4.....	0.77 (0.91)	0.66 (0.78)	0.71
5.....	0.96 (0.79)	0.66 (0.54)	0.75
6.....	1.18 (1.20)	0.68 (0.69)	0.83
7.....	1.38 (1.22)	0.72 (0.63)	0.96
8.....	1.70 (1.20)	0.88 (0.70)	0.82
9.....	2.32 (3.13)	1.21 (1.63)	1.09
mean.....	1.66 (1.70)	0.80 (0.83)	0.86

in the first column. As an estimate of the coefficient of turbulence, the mean of the second column is less good than is the mean of the third column where the trend is even less well marked, though these two means are almost identical. Comparison of the second and third columns indicates that in the upper

part of the clinolimnion, the value of $\frac{d\Theta_b}{dt} \cdot \frac{\partial z}{\partial \bar{h}}$ is

too low to give a reliable coefficient of turbulence, thus implying that part of the heat brought through the horizontal planes of this region is lost by absorption in the mud; this is also implicit in the ex-

ponential arrangement of $\frac{\partial \Theta}{\partial t}$ in the clinolimnion.

The nine-meter level on the other hand may not be truly clinolimnetic, but the difference between 0.96 at 7 m. and 1.09 at 9 m. in the third column is not great enough to warrant excluding the latter value in the clinolimnetic estimate of the coefficient of turbulence. If the estimates of the second column are continued to greater depths they increase, but, as has been shown in the previous section, it is very doubtful if pure turbulence can be evoked to explain heating at depths below the clinolimnion. In the next paragraphs the possibility of another mechanism of heating is suggested which is particularly significant as it explains the fact that the residuals apparently due to non-turbulent heating are greatest in the deepest water, and are best demonstrated in the most eutrophic lake of the three under consideration.

ROLE OF DENSITY CURRENTS

1.11.1. It has long been known, from the observations of Buchanan (1879) and very many subsequent observers, that heating of lakes can occur under an ice cover, and that the bottom temperatures resulting from such heating may rise above 4.0° C.⁶ This is known to occur in Lake Mendota (Birge and Juday, 1911, data for March 6, 1909) as well as in a number of other lakes, not involved in the present discussion; a concise summary of the relevant literature has been presented by Yoshimura (1936a). Apart from crenogenic meromixis, two principal factors play a part in the phenomenon. Firstly, heating of water by

⁶ Buchanan's example may be a meromictic lake.

solar radiation at the surface, particularly in shallow water, sets up a thermal density current as the temperature of the cold water approaches 4.0° C. Secondly, the passage of heat stored in the mud in the summer into water cooled to below 4° C. similarly will cause a density current carrying heat towards the deeper part of the lake. These two factors were first considered quantitatively by Birge, Juday and March (1928). In order to explain the rise in temperature above 4.0° C. it is necessary to suppose that a chemical as well as a thermal increase in density in the water immediately over the mud is involved. This is clearly shown in Table 8, giving the temperatures, alkalinities and oxygen contents of Linsley Pond, before and after the breaking of the ice in the spring of 1936. It is extremely doubtful if there was a full circulation in the spring of 1936. The very high bottom temperature and alkalinity observed at the end of winter stagnation in this year were undoubtedly due to the exceptionally hard winter and the resultant persistent ice sheet. Subsequent years, in which the ice has never lasted as long as in 1935-36, have shown similar phenomena but not on such a marked scale. It is highly probable that the initiation of biogenic meromixis takes place after exceptionally severe winters when the spring circulation is incomplete and when almost all the accumulation of dissolved substances of a long winter stagnation can be added to the accumulation developed in the succeeding summer.

TABLE 8. Thermal and chemical stratification of Linsley Pond after about 3 months under ice (freezing occurred between December 14 and 27).

		0 m.	5 m.	8 m.	12 m.	14 m.	14.5 m.
Dec. 14, 1935 No ice.	Temp.	3.50	3.50	3.50	3.51		3.51
	HCO ₃	68.6	69.1	68.3	70.0		69.5
	O ₂	10.37	9.89	10.05	9.89		9.76
Mar. 7, 1936 50 cms. ice	Temp.	1.68	4.12	4.21	4.21	4.70	
	HCO ₃	8.9	72.5	76.9	76.8	84.9	
	O ₂	12.13	5.08	3.22	3.09	—	
Mar. 21, 1936 Almost no ice	Temp.	4.83	4.58	4.43	4.76		4.73
	HCO ₃	56.0	58.0	72.7	75.4		85.4
	O ₂	8.50	8.19	4.61	3.15		0.10
Mar. 28, 1936 Ice free	Temp.	7.68	6.48	5.42	5.21		5.15
	HCO ₃	60.6	62.7	62.8	64.3		73.0
	O ₂	9.55	7.56	8.10	7.86		4.17

1.11.2. Alsterberg (1930, 1931) has pointed out that the concept of profile-bound density currents need not be limited to winter stagnation. Since the mud is colder than the water in summer, the thermal density current, as Alsterberg points out, is a cold descending current. If, however, sufficient dissolved material passes into the water immediately over the mud of the slope of the basin, this dissolved material may cause the water to flow down the slope to a level at which the free water has a lower temperature, but not a greater density, than the water of the current; in this way heat can be brought down to the level in question. In view of the fact that chemical density currents must clearly be involved in the winter heat-

ing of all holomictic lakes in which the bottom water rises above 4.0° C., it seems probable that part of the heat delivered in summer to the lowest part of the bathylimnion of Linsley Pond and Lake Mendota is also carried by such currents. In the case of Lake Quassapaug, where, in spite of the striking development of the bathylimnion, an increase in alkalinity and possibly in phosphate is not clearly indicated below 15 m. until the end of August, conductivity studies might well demonstrate an earlier bathylinnetic increase in total concentration. The greatest objection to accepting the hypothesis that density currents are entirely responsible for the formation of the bathylimnion is derived from an examination of the early weeks of heating in Lake Mendota (e.g., Fig. 5), where the region appears to be developing very rapidly. For the earliest date (first week in June) for which a reliable value of the clinolimnetic

coefficient can be obtained, $\frac{\partial \theta_{nt}}{\partial t}$ has the following values:

18 m.	0.55° C. per month
20 m.	0.83
22 m.	1.08
23 m.	1.18.

These seem rather high for a period so early in chemical stratification. No other non-turbulent mechanism⁷ can be suggested and it is possible that early in the summer in Lake Mendota the vertical variation of the coefficient is more marked than at later dates or in the other two lakes. Figure 9 indicates diagrammatically the mechanisms of heating believed to occur in a stratified lake.

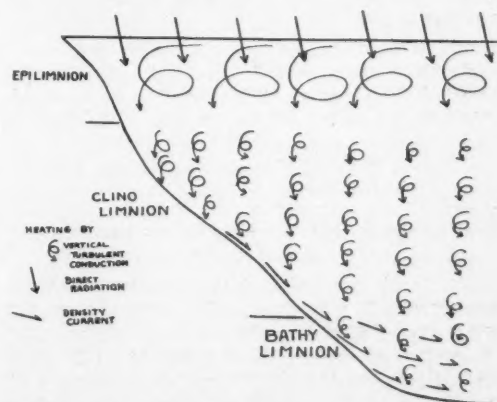


FIG. 9. Diagrammatic scheme of the heating of a lake by radiation, turbulent conduction, and density currents according to the theory developed in the present paper.

⁷ Biological oxidation must produce some heating. A rise of 0.1° per month, however, corresponds to 100 cal. per litre per month, i.e., to an oxygen uptake of about 20 cc. per litre per month or 28.6 mgrms. per litre per month. Reference to the value of the non-turbulent rate of change shows that 0.1° C. is a reasonable figure, but as is indicated in 2.5.2, a metabolic rate of the order implied is about five times too great in the case of Linsley Pond. Cooling by the upward current displaced by density currents will be negligible in the clinolimnion on account of its great volume compared with the bathylimnion.

GROTE'S REGIONAL MODULUS OF TURBULENCE

1.12. The Quassapaug data have been little used in the preceding discussion as they are clearly inadequate, owing to the limited number of dates on which readings were taken, and the considerable accidental oscillations of temperature observed at some levels. At 10 m. in particular, the correlation of temperature with time is only 0.418, which, with eight sets of observations, is entirely insignificant statistically. Such fluctuations in the thermocline are to be expected in a fairly large sharply stratified lake. Omitting the ten-meter level, a fair exponential fall is obtained between eight and fourteen meters, below which depth the bathylinnion is well defined. The seven meter level shows a remarkably low value

of $\frac{\partial \theta}{\partial t}$ which, however, seems to be reliable. Taking

the clinolimnion as lying between eight and fourteen meters the coefficient of turbulence may be estimated as 1.07, which is not significantly higher than that in Linsley Pond. Both lakes have essentially the same range of hypolimnetic temperatures, and differ in this respect, as in their clinolimnetic coefficients of turbulence, most strikingly from Lake Mendota. Now Grote (1934) has pointed out, that making certain reasonable assumptions, the square of the depth of the thermocline, i.e., of the thickness of the epilimnion, can be used as a measure of the turbulence of the latter so that in a geographically and climatically uniform lake-district, a modulus of turbulence can be established, based on some lake taken as unity. Taking the thermocline as at four meters in Linsley Pond and eight meters in Quassapaug, we find that though the clinolimnetic coefficients of turbulence are practically identical, the epilimnetic modulus in Quassapaug is four times that in Linsley Pond, taken as unity. This epilimnetic difference is to be expected in view of the very much greater area of the former lake (1.72 km² as opposed to 0.094 km²); that the clinolimnetic coefficients should bear no apparent relation to the area is more remarkable.

COMPARISON WITH THE RESULTS OF PREVIOUS INVESTIGATORS

1.13. In his classical work on turbulent transport, Schmidt (1925) gives values for A in the Lunzer Untersee, calculated from the total heat income below a given isobath by means of equation (11). The computations were made for 5 m., 10 m., 15 m., and 20 m. In April there is a more or less constant value of $A = 2$ at least down to 15 m. In July the value at 5 m. had fallen to 0.18; at 20 m. to 0.01. The deep water summer values are clearly of the same order of magnitude as in the clinolimnion of Lake Mendota ($A = 0.0252$). The present investigation was well advanced before Schmidt's work could be consulted, and for this reason McEwen's more elaborate treatment was taken as a convenient starting point. The more detailed analysis made possible by McEwen's treatment of equation (1) has, however, amply justified the present approach. The only other

estimate of the turbulence coefficient in any lake is that made for Lake Balaton by Defant (1932), who used a most ingenious method based on the discrepancy of the observed period of the longitudinal seiche and the period calculated by classical methods. The resulting value of the coefficient of turbulence (i.e., the coefficient of eddy viscosity), $A = 45$, seems extraordinarily high, though within the range of values possible in the ocean.

ALKALINITY AS AN INDICATOR OF WATER-MOVEMENTS AND OF THE METABOLIC CONDITION OF THE HYPOLIMNION

THE DATA

2.1. Along with the temperatures taken in Linsley Pond and Lake Quassapaug, a series of determinations of the alkalinity by methyl orange titration was obtained. Lake Quassapaug contained too little bicarbonate to be of any great interest in the present study, and the analysis of the data is restricted to that from Linsley Pond. Saunders' method (1927) of using a standard prepared by saturating distilled water with carbon dioxide was employed in all titrations. The results are expressed as milligrams of HCO₃ per litre.

THE FORM OF THE ALKALINITY CURVE

2.2.1. In a preliminary communication (Hutchinson, 1938) it was pointed out that when the mean alkalinity, at any depth in Linsley Pond over a period long enough to avoid accidental disturbances due to distortion of the stratification, is plotted against depth, the resulting curve bears an evident relationship to the morphometry of the lake basin. This is most clearly seen when the morphometry is expressed as the variation of mud surface per unit volume of water at any level; the curve showing the mean radius of the lake is less instructive (Fig. 10), but indicates essentially the same relationship. Owing to an error in the method of calculating the relation of the area

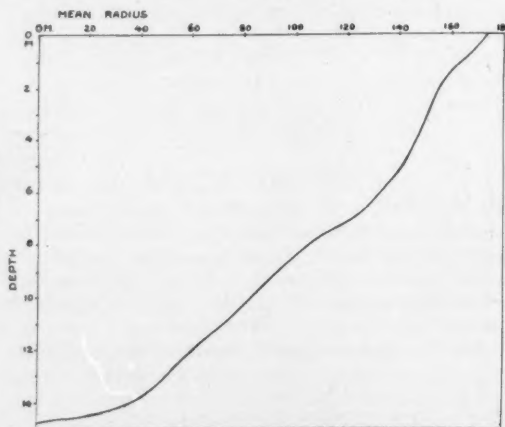


FIG. 10. Linsley Pond. The mean radius plotted against depth, or generalized profile. Note the well-developed shelf at 7 m. and the suggestion of a second shelf at about 11 m.

at any depth of the mud surface to the volume at that depth, it was supposed that this only held when the area was projected onto a plane surface. Actually the ratio of the projected element of area to the corresponding element of volume is practically the same as the ratio of the actual element of area to the element of volume. In Figure 11 the mean alkalinity for the whole period from the beginning of June to the end of August 1937 is plotted against depth, as is the ratio of the element of area of mud surface to element of volume at that depth. The latter curve was obtained by drawing a curve relating area to depth, differentiating by means of the Richards-Roope (1930) tangentmeter and dividing the value of the derivative by the area at each depth

$$\frac{dA}{dz} \cdot \frac{1}{A} = \frac{dA}{dz} \cdot \frac{dz}{dV} = \frac{dA}{dV}$$

Interpolation of half-meter points has been used and is probably justified, though the finer form exhibited as the result of this process (e.g., the minimum at 8.5 m.) cannot be shown by the alkalinity curve based

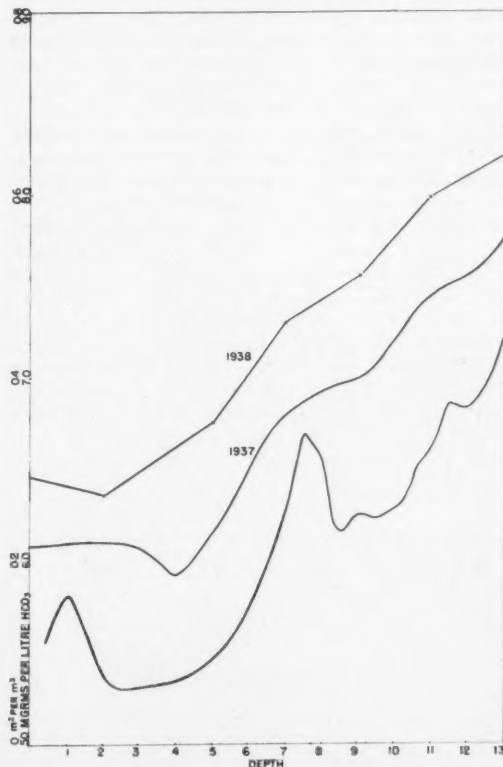


FIG. 11. Linsley Pond. Lowest curve, the morphometric curve, showing the variation of $\frac{dA}{dV}$ with depth. Middle curve variation of mean bicarbonate content in milligrams per litre with depth, for June-August, 1937. Topmost curve, the same for 1938. Note that in spite of the large intervals in the 1938 curve, the variation in slope in the hypolimnion is similar in both years.

on points one meter apart. The correspondence of the form of the curves is immediately apparent. In 1938, the work on other lakes, particularly Lake Quassapaug, made such an extensive series of observations in Linsley Pond impossible. A series of determinations, for the most part at two-meter intervals, was made. The plot of the mean of this series shows that the same phenomenon was occurring in both years, though its exact nature is less evident in the less extensive 1938 series than in the 1937 series. The significance of the epilimnetic differences in the two years is uncertain but not relevant to the present discussion. The relationship observed in the first year is therefore a general one, characteristic of the lake. As was pointed out in the preliminary communication, the only reasonable explanation of the relationship is that the bicarbonate originates in the bottom mud, and is carried into the free water by horizontal currents, probably of variable direction, which are sufficiently rapid to permit the development of a pattern in the alkalinity distribution in spite of the slight turbulent mixing in a vertical direction necessarily postulated for the distribution of heat. Further analysis indicates, however, that the problem of the alkalinity curve is more complex than at first appeared, though nothing has yet been discovered that casts doubt on this primary hypothesis.

2.2.2. When the morphometric relationship of the alkalinity curve had been established it was natural to inquire whether any similar distributions had been observed by previous investigators, and to attempt to obtain information from other Connecticut lakes that could be used in confirming the observations made in Linsley Pond. The results of this inquiry have so far been disappointing, as it would seem that certain special conditions must be satisfied before the relationship can become apparent. Soft water lakes do not contain enough bicarbonate to give any reliable variation of alkalinity with depth; conductivity determinations might provide interesting data in such cases. In the majority of hard-water lakes, containing far more bicarbonate than does Linsley Pond, there is a tendency for the alkalinity to fall, in the upper hypolimnion at least, during the course of stagnation. This is apparent in some of the data tabulated by Birge and Juday (1911) for Lake Mendota, and was observed by Dr. Deevey in the hard water lakes examined in Connecticut and New York State in the hope of throwing further light on the present problem. This fall is possibly due largely to bacterial precipitation of calcium carbonate, though Williams and McCoy (1934) who have investigated the matter, were unable to obtain definite proof of this. Any such disturbance naturally renders the morphometric effect unobservable. It is, moreover, obviously necessary for the development of the effect that the lake should be productive enough to produce adequate carbon dioxide in the mud, deep enough to be well stratified, small enough for the mud to have an appreciable influence on the free water and of such a shape that some conspicuous morphological feature can be easily recognized in the alkalinity curve if the relationship

holds. It is evident that Linsley Pond is exceptional in the coincidence of all these requirements. The Schleintsee described by Einsele and Vetter (1938) also fulfills these requirements and probably exhibits comparable phenomena, but the number of points on the alkalinity curve and the published information on the morphometry of this lake, though suggestive, are not sufficient to permit a final conclusion.

THE RATE OF CHANGE OF ALKALINITY WITH TIME

2.3.1. Since the alkalinity is uniform throughout the entire range of depths at the time of the spring turn-over, the determinations for any one date give a rough idea of the speed at which bicarbonate has accumulated at any depth since the over-turn, and it is important to remember that the characteristic pattern, strikingly shown in the mean curves, is really an expression of differences in the rate of accumulation at different levels. Though the curves give unequivocal evidence of the general distribution of rates of increase, they cannot be used in further analysis. Even in Linsley Pond there appear to be occasions on which a part of the bicarbonate can be lost at any level, though the amount so lost is small and technical error cannot be altogether excluded. A few irregularities of this sort near the beginning or end of the series may produce a great difference in the slope of the best fitting line but little difference in the mean for that level. In the preliminary communication it was suggested that rapid rises in bicarbonate content tend to occur at a time when the stability of the epilimnion is low; the observations made in 1938 cast some doubt on this supposition. It is, however, certain that the rise in bicarbonate content does not occur at a constant rate; apart from the embroidery previously attributed to stability changes, there is a clear general tendency for the curve relating alkalinity and time at any depth to have a sigmoid form. Since the gradient is steepest at the bottom, sampling errors will be greater at the bottom and not in the thermocline and upper clinolimnion, as is the case with temperature readings. Computation of mean rates from the available data, by the method employed in 1.1.2. is therefore unfortunately somewhat more questionable than is the case with temperature; the resulting rates are likely to be the least reliable near the bottom, rather than in the metalimnion. Such mean rates, must, however, be used and in general show the same trends as do the means, except near the bottom, where wide departures occur, as at 11 m. and 13 m.; here the mean rates, based on a more complex procedure than the simple means, must be regarded as suspect.

2.3.2. Considering only the clinolimnion between 4 m. and 12 m. over which the clinolimnetic turbulence coefficient may be applied ($\mu^2 = 0.86$) it is possible to calculate what part of the observed change in alkalinity is due to turbulence (Fig. 13). To do this it is necessary to obtain the second derivative of the curve relating mean alkalinity to depth. This was done mechanically, by means of the Richards-Roope tangentmeter, the first derivative curve being obtained and a second differentiation carried out on it. The

values, for the different depths, of $\frac{\partial^2[\text{HCO}_3]}{\partial z^2}$, in milligrams per litre per meter per meter are then multiplied by 0.86 to give the calculated rate of change due to turbulence; subtraction from the observed values $\frac{\partial[\text{HCO}_3]_{\text{at}}}{\partial t}$ gives the non-turbulent rate of change $\frac{\partial}{\partial t}$.

Since the observed turbulence coefficient is not very large in comparison with the coefficient of molecular heat conduction, some error is certainly introduced by neglect of molecular diffusion. The procedure also introduces other opportunities for small errors. The fall in the value of the non-turbulent rate at seven meters would not appear if a very slight alteration in the drawing of the curve relating mean alkalinity to depth were made prior to the first differentiation; such an alteration might be justified, as the position of the inflection point of the curve is to a large extent arbitrary. In spite of this irregularity there is a very evident step-like region in the curve between 6 and 8 m. corresponding to the maximum in the morphometric curve between 7 and 8 m. Both curves undoubtedly rise steeply beyond nine meters. The general superposition of the curve for the non-turbulent rate of change on that for the observed total clearly indicates the greater importance of horizontal and possibly profile-bound currents as opposed to vertical mixing in determining the chemical structure of the lake.

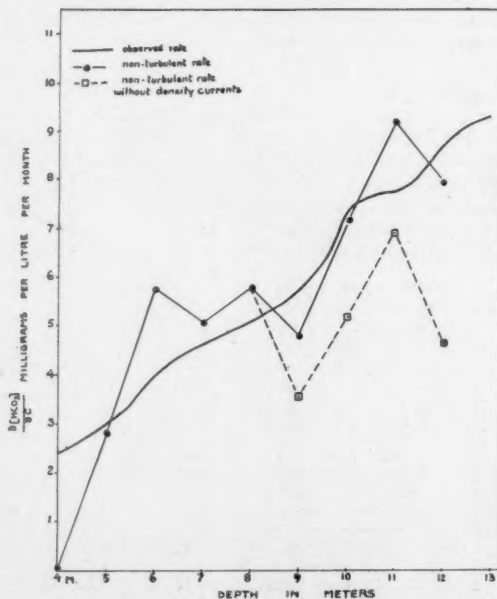


FIG. 12. Linsley Pond. Smooth unmarked curve, the mean rate of increase in bicarbonate concentration with time plotted against depth for 1937. Circles joined by unbroken lines, the non-turbulent rate of increase plotted against time. Squares joined by broken lines, the non-turbulent rate less the supposed contribution of density currents.

2.3.3. Assuming now the validity of the argument presented in 1.10.3., we may extend the process into the bathylinnion, calculating first the rate of change due to turbulent mixing, and from the observed value

obtain the residual $\frac{\partial[\text{HCO}_3]_{\text{nt}}}{\partial t}$. In view of the

uncertainties inherent in the fit of the temperature curve, this procedure can hardly be valid below 12 m. According to the argument presented in 1.11.2. part of the rise in alkalinity at all bathylimnetic levels is due to density currents running down the slope of the lake basin to levels appropriate to their densities. Assuming that the non-turbulent rise in temperature is due to such currents, a rate of change of 0.1°C . in unit time may be taken as equivalent to a rate of decrease in density of 0.000005 in unit time. Using the figure given in 1.8. for the difference in density between the water of Linsley Pond and distilled water, this rate of decrease is balanced by an increase of 2.8 mgrms. per litre of HCO_3 in unit time, so that it is possible to compute the amount of bicarbonate brought in by the density currents. Subtracting this from the non-turbulent rate gives the rate at which the concentration of bicarbonate, derived from the level in question, rises. In view of the fact that the density probably depends on substances other than and varying independently of bicarbonate, no great accuracy can be attached to the final estimate of the output from the mud at each level of the bathylinnion, but the results presented in Table 9 and shown graphically in Figure 12 are probably of the correct order of magnitude. The complete analysis described above is given in Table 9.

ESTIMATE OF BICARBONATE OUTPUT FROM UNIT MUD SURFACE

2.4. A further treatment of the alkalinity curve is now possible by estimating the rate at which bicarbonate must leave the mud to cause the observed non-turbulent rate of change at each level. Below 9 m. the residuals, after subtracting the contributions due to density currents, should be used if the latter

TABLE 9. Analysis of Rate of Change of Bicarbonate Concentration (all figures in mgrms. per litre per month unless otherwise stated).

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
	$\frac{\partial^2[\text{HCO}_3]}{\partial x^2}$	$\frac{\partial^2[\text{HCO}_3]}{\partial x^2}$	$\frac{\partial[\text{HCO}_3]}{\partial t}$	$\frac{(3) - (2)}{\partial t}$	$\frac{\partial \theta_{\text{nt}}}{\partial t}$	$(5) \times 27.5$	$(5) - (6)$	$\frac{dA}{dV}$	$(4) \cdot \frac{dV}{dA}$	$(7) \cdot \frac{dV}{dA}$
	mgrms. per litre per m. per m.	=turbulent rate of change	=observed rate of change	$\frac{\partial[\text{HCO}_3]_{\text{nt}}}{\partial t}$	$^\circ\text{C}$ per month	rate of change of HCO_3 due to density currents	rate of change of HCO_3 due to hori- zontal movements	m^2 per m^3	estimates of rate of output into horizontal current grms. per m^2 per month	estimates of rate of output into horizontal current grms. per m^2 per month
4....	2.80	2.41	2.42	0.01				0.0685	0.15	
5....	0.29	0.25	3.03	2.78				0.0904	30.8	
6....	-2.05	-1.76	4.00	5.76				0.1461	22.4	
7....	-0.49	-0.42	4.60	5.02				0.2571	19.5	
8....	-0.80	-0.69	5.09	5.78				0.3069	18.8	
9....	+1.05	+0.90	5.70	4.80	0.047	1.3	3.5	0.2507	19.1	14.2
10....	+0.09	+0.08	7.28	7.20	0.075	2.0	5.2	0.2558	28.1	20.3
11....	-1.78	-1.53	7.70	9.23	0.083	2.3	6.9	0.3230	28.5	21.4
12....	+0.96	+0.83	8.77	7.94	0.120	3.3	4.6	0.3651	24.6	12.6

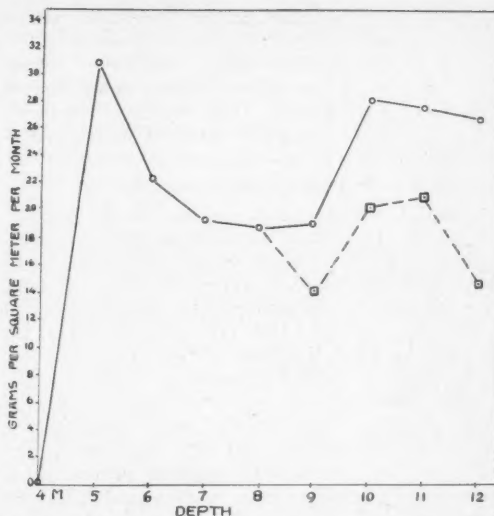


FIG. 13. Linsley Pond. Circles joined by unbroken lines, the rate of output of bicarbonate from unit area of mud surface in 1937, uncorrected for the effect of density currents. Squares joined by broken lines, the same less the increase in alkalinity due to density currents.

exist; as some doubt may be felt as to their reality, both the total non-turbulent rates and the rates from which the contribution of density currents have been subtracted are used. These, when multiplied by the reciprocal of the morphometric factor, $\frac{dA}{dV}$, used in

preparing the lower curve of Figure 11, give the required values in grams per square meter per month. There is clearly a tendency to a bimodal distribution with respect to depth (Fig. 13). If the density current hypothesis be accepted the upper mode is clearly the best developed; the fall between 7 and 9 m. may in part represent bicarbonate lost from these layers and delivered to the lower layers by the

density currents. If this is accepted there is probably a progressive decrease from 5 to 12 m. in the rate of removal of bicarbonate from the mud surface into the lake water. This progressive decrease may well be an expression of the vertical variation of the velocity of horizontal currents transporting the substance in question.

CARBON DIOXIDE ANOMALY

2.5.1. A very important corollary to the fact that the greater part of the variation in the bicarbonate content of the hypolimnion is to be accounted for by horizontal movements of water from the mud-water interface towards the center of the lake, may now be tentatively discussed. Ohle (1934) has considered the quantity by which the observed free CO_2 is in excess or in defect of the amount expected from the actual oxygen deficit (ΣO_2), a respiratory quotient of unity being assumed. This anomaly may be called the free carbon dioxide anomaly (ΔCO_2). It is clear, however, that the free carbon dioxide represents only a part of the metabolic carbon dioxide produced in the hypolimnion, since half of the carbon dioxide present in the bicarbonates of non-volatile bases and the whole of the bicarbonates present in equilibrium with the ammonium ion is to be regarded as metabolic. The metabolic carbon dioxide anomaly ($\Delta'\text{CO}_2$) is therefore probably of greater interest than the anomaly considered by Ohle. One series of carbon dioxide determinations only is available for Linsley Pond, made on September 20, 1937. In order to determine the metabolic CO_2 , the increase in alkalinity since the lake was of uniform alkalinity, 143 days previously, on April 30, 1937, has been computed. Data for volatile alkali are not available for September 20, but figures for October 2, 155 days after the initial date, are available and have been multiplied by 0.923 to correct approximately for the later date. The data derived in this way are set out in Table 10 and Figure 14. It will be observed that while the original data for carbon dioxide show a vertical distribu-

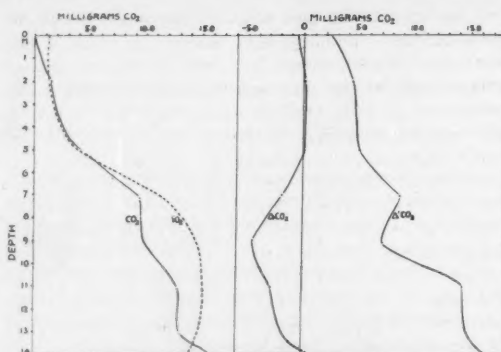


FIG. 14. Linsley Pond. Left, free CO_2 (solid) and CO_2 equivalent of oxygen deficit; right, free carbon dioxide anomaly (ΔCO_2) and metabolic CO_2 anomaly ($\Delta'\text{CO}_2$), all for September 20, 1937.

2.5.2. Since the only probable source of the excess carbon dioxide represented by $\Delta'\text{CO}_2$ is the anaerobic metabolism of the mud, and since the observations made by Riley and confirmed less extensively in the present investigation show that the oxygen consumption of the water of the hypolimnion in a dark bottle *in situ* is sufficient to account for the oxygen deficit, we can clearly divide the metabolic changes that affect the free water of the hypolimnion into two categories. One category comprises changes taking place in the water *in situ* and may be called *hydrometabolism*; the other category, comprising changes in the most superficial layer of the mud or at the mud-water interface, insofar as such changes affect the free water, may be termed *pelometabolism*. Substances, the concentration of which is primarily due to hydrometabolism, will show no morphometrically determined inflections on the curve of vertical distribution; this is most conspicuously true of the oxygen curve. Substances whose concentration is primarily determined by the pelometabolism, will show such inflections, as in the case of the curve of vertical distribution of alkalinity. Since in succeeding sections of the present work the great importance of pelometabolic changes is emphasized, it is of interest to attempt to obtain some measure of the relative magnitudes of the two metabolic categories. The mean value of the metabolic carbon dioxide anomaly on September 20 for the whole hypolimnion, below 4 m., duly weighted for the volume of each layer, is 7.98 mgrms. per litre. This corresponds to an anaerobic production of pelometabolic carbon dioxide of 1.68 mgrms. per litre per month. Though this estimate is liable to error in that neither is information available as to the departures from a linear relation between the anomaly and time or from a value of unity for the respiratory quotient, nor has loss of CO_2 by turbulent transport been considered, it may be taken as an approximate and probably minimal estimate of the pelometabolism of the hypolimnion. Estimation of the hydrometabolism is somewhat more difficult. Since it appears (Riley, 1940) that the low and relatively constant oxygen concentrations observed in the hypolimnion during

TABLE 10

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Depth	HCO_3^- in April 30-Sept. 20	Volatile alkali (0.923 x 2 Oct. data)	CO_2 of non-vol. alkali (2) x (3) x	CO_2 of vol. alkali (3) x	Free CO_2	Metabolic CO_2 (4) + (5) + (6)	ΣO_2 x 1.375	ΔCO_2 (6) - (8)	$\Delta'\text{CO}_2$ (7) - (8)
0	9.4	0	3.4	0	0.07	3.5	1.3	-1.2	2.2
2	11.9	0	4.3	0	1.5	5.8	1.4	0.1	4.4
5	12.6	0.8	4.3	0.6	3.9	8.8	3.8	0.1	5.0
7	25.1	3.6	7.8	2.6	9.5	19.9	11.3	-1.8	8.6
9	27.0	5.4	7.8	3.9	9.7	21.4	14.2	-4.5	7.2
11	36.6	9.3	9.9	6.7	12.7	29.3	15.1	-2.4	14.2
13	36.2	10.2	9.4	7.4	12.9	29.7	14.8	-1.9	14.9
14	35.1	(10.2)	9.0	7.4	13.6	30.0	13.8	0.2	16.2

tion comparable to that of the bicarbonate ion, so reflecting the morphometry of the basin, this step-like distribution is much accentuated in the curve for the metabolic carbon dioxide anomaly.

the latter half of the summer represent a steady state between photosynthesis and oxidative consumption, the oxygen deficit cannot be used in a way comparable to the metabolic anomaly. Riley's experiments indicate that on an average the water of the lake when placed *in situ* in a dark bottle, consumes oxygen at an initial rate of about 4 mgrms. per litre per month.⁸ This figure was obtained during the period between October and June and *a priori* might be expected to be too high when applied to water containing very little oxygen. A few data obtained in September, 1937, suggest that this is indeed the case; on the other hand a series obtained at the beginning of August shows higher values. In default of better information, Riley's figure may be provisionally accepted; it is certainly of the correct order of magnitude. 4 mgrms. O₂ correspond to 5.5 mgrms. of carbon dioxide produced per month, assuming again a respiratory quotient of unity. The pelometabolism, as measured by the metabolic CO₂ anomaly for the whole hypolimnion, would therefore appear to constitute about one fourth of the total metabolism as measured by the total rate of CO₂ production of the hypolimnion. This estimate is admittedly very rough, but is of value in showing that, owing primarily to the horizontal current system, the biochemical conditions of the hypolimnion as a whole may be considerably influenced by events taking place in the insignificantly small volume of mud in immediate contact with the water. In any consideration of substances, which unlike carbon dioxide cannot be produced in appreciable quantities in the free water, the importance of the pelometabolic contribution is vastly more important. In large lakes the ratio of the two metabolic categories will be much more in favor of hydrometabolism than in Linsley Pond, and all substances of exclusively pelometabolic origin will be present in lower concentrations. The principle developed in the present section is in fact an attempt to give quantitative expression to one aspect of Strom's (1932) generalization that productivity is a function of the ratio of volume to bottom surface. The mechanism by which the mud affects the free water in a stratified lake is of course entirely incomprehensible without a knowledge of the movement of dissolved substances by horizontal currents.

BASES IN EQUILIBRIUM WITH BICARBONATE

2.6.1. A few observations of the nature and distribution of the bases present in the water of Linsley Pond may not be out of place. Calcium has been determined essentially as recommended by Meloche and Setterquist (1933). Magnesium has been determined by Barnes' (1928) modification of Kolthoff's colorimetric method, using titan yellow after determination of the calcium, the concentration of calcium in the sample being adjusted to correspond to a known concentration in the standards. Total iron has been determined following Standard Methods of Water Analysis (8th ed. American Public Health

⁸ This rate is not maintained, so that the oxygen concentration of water isolated at the spring overturn in a dark bottle hung in the hypolimnion never falls as low as that of the free water surrounding the bottle some months later.

Association, 1936), and total manganese by Winkler's method, following Maucha (1932). The titan yellow method for magnesium is very sensitive, not perhaps as accurate as might be desired; on one occasion (0 m. August 22, 1937) it gave results that are obviously too low and have been rejected.

2.6.2. Owing to the defective magnesium determination at the surface for August 22, and the presence of a large amount of decaying *Anabaena* liberating ammonia, after copper sulphate treatment, on August 5, the series for the surface water is less good than at 5 m. The mean value of the sum of the calcium and magnesium at the latter depth between July 12 and September 16, 1938, was 1.181 milli-equivalents per litre, the bicarbonate content at this depth and time 1.144 milli-equivalents per litre. The corresponding surface values with the defective dates omitted are 1.075 milli-equivalents for calcium and magnesium, 1.049 for bicarbonate. At these depths, therefore,

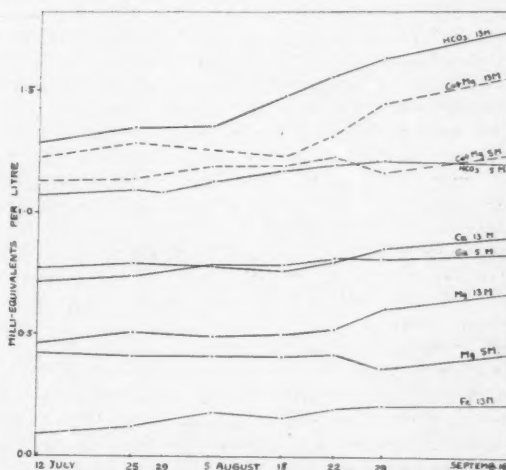


FIG. 15. Linsley Pond. Variation of bicarbonate and calcium and magnesium at 5 and 13 m., and of iron at 13 m. throughout the latter half of stagnation in 1938. (Milli-equivalents per litre.)

there is sufficient of the alkali earth kations to balance the whole of the bicarbonate and with small amounts (3-4%) in equilibrium with other anions (probably sulphate and silicate) as well. At nine meters the combined calcium and magnesium, give a mean of 1.289, the bicarbonate 1.343 milli-eq. per litre. The excess of bicarbonate is even more strongly marked at 13 m. where the mean for the two kations is 1.332, for the bicarbonate 1.490 milli-eq. per litre. The graphical presentation (Fig. 15) of the condition at 5 m. and 13 m. indicates how the excess of bicarbonate over calcium and magnesium develops as stagnation progresses. A few ammonia determinations and numerous data on the iron content show that there are present more than enough ammonium and ferrous ions to balance the bicarbonate under such conditions. Thus on August 5 at 13 m. there was present

Mg	0.484 milli-eq. HCO_3	1.357 milli-eq.
	per litre Sum of	per litre
Ca	0.770 "	bases 1.499
NH_4	0.074 "	Difference 0.142
Fe (as Fe · ·)	0.171 "	

At this time some of the iron is probably in a form other than ferrous ions, but a small quantity of manganous ion may have been present. It is clear that anions other than the bicarbonate also increase during the stagnation; presumably silicate, which has not been studied in the deep water of the lake, is the most important. In 1937 it was believed (Hutchinson, 1938) that the whole of the rise in the bicarbonate concentration in the deep water was due to ferrous and ammonium bicarbonate, since the 1937 analyses show a deficiency of bases in the deep water; it is clear that the calcium and magnesium determinations of these preliminary studies were too low.

2.6.3. With the exception of sodium, studied only on September 20, 1937, when about 1 mgrm. per litre was present at all levels, which, as is to be expected (Yoshimura, 1933) shows no clear vertical stratification, there is a marked tendency for all the bases present (Ca, Mg, NH_4 , Fe, Mn)⁹ to increase in concentration in the hypolimnion during stagnation. In the cases of magnesium, ammonia and iron, this increase progresses most rapidly at the bottom, less so at lesser depths. A few representative determinations for the first two substances are presented in Figure 18, the question of iron is discussed in 3.7. Calcium shows a tendency to higher values in the middle water than at the bottom during August and September, becoming regularly stratified only at the end of stag-

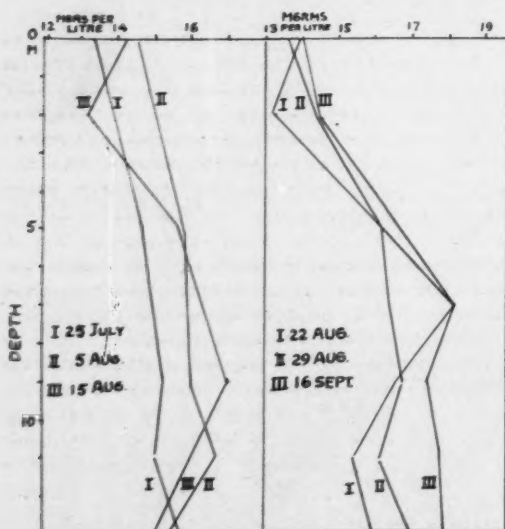


FIG. 16. Linsley Pond. Vertical distributions of calcium.

⁹ A slight stratification of sulphate was observed on September 20, 1937 (0 m. 0.75, 2 m. 0.68, 5 m. 1.47, 9 m. 1.64, 13 m. 1.70). On October 13, 1938, 0.05 mgrms. per litre of titanium was detected in 13 m. water; this may have been in suspension.

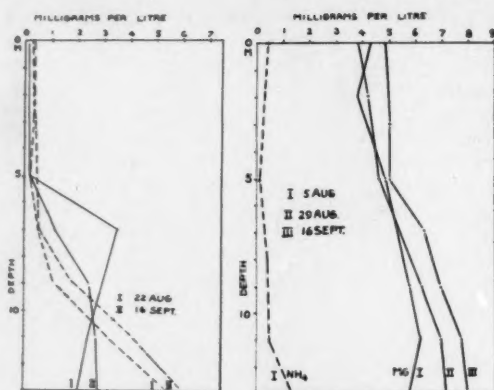


FIG. 17. Linsley Pond. Vertical distributions of manganese (solid) to show the difference in stratification from that exhibited by total iron (broken).

FIG. 18. Linsley Pond. Vertical distributions of magnesium (solid lines) and of ammonia (broken line) in the latter half of stagnation in Linsley Pond, 1938.

nation (Fig. 16). The concentrations at the different levels vary rather irregularly, and though the high maximum at 7 m. on August 22 was checked and is certainly not due to technical error, its absence on August 29 may be due to sampling error as it reappears on September 13. No great significance should be attached to the rather meagre data available, but they suggest that calcium passes into solution more easily in the layers poor in iron than the layers where, in what will be defined (3.4) as phase III of stagnation, much ferrous iron is found. The data given in Figure 17 for manganese show very considerable and well-established variations, with an intermediate maximum on August 27 very much like that for calcium. Small maxima of calcium in the upper hypolimnion are recorded in some of Ohle's (1934) analyses of Baltic lakes, while apart from the extraordinary metalimnetic maximum of manganese in Ranu Klundungan in Java, Ruttner (1931) has recorded smaller maxima in intermediate water not unlike those reported above. At present it is merely desirable to call attention to the chemical activity exemplified by the changes in manganese, and to a less extent calcium, concentration, and to point out that if the density current hypothesis of 1.11.2 be accepted, the water at the bottom has gained some of its alkalinity at higher levels, but has subsequently passed over a considerable mud surface that may provide great opportunities for base exchange. It is hoped in the future to obtain more data on the variations of these substances.

COMPARISON WITH THE RESULTS OF OTHER INVESTIGATORS

2.7. The horizontal water-movements of the hypolimnia of stratified lakes have been studied by Wedderburn and Watson (1909), Wedderburn (1910), Möller (1928, 1933), Whipple (1927) and others, but too little information exists to permit any empirical generalizations of value in the present

study, other than to state that the existence of such currents is well established. Defant's (1932) interesting theoretical treatment assumes a steady state resulting from the action of the wind on the lake surface, and deduces two complete circulation systems, one in the epilimnion, one in the hypolimnion. This implies zero horizontal motion (dead water) at a certain depth in both regions. The type of circulation deduced by Defant does not seem to fit in very well with the meagre observations available, which suggest that a steady state is very rarely achieved. Recently Elster (1939) has applied the methods of dynamic analysis used in Oceanography, to a study of the deep-water currents of Lake Constance. In general he finds a decrease in the motion between any two stations in a transverse profile with increasing depth, except near the shores of the lake. A current system of this sort may well be developed only in large lakes, but would fit the observed changes in alkalinity discussed in the present paper. The direct measurements of both Wedderburn and Möller, however, suggest a more irregular type of distribution of velocities. Hypolimnetic water-movements have been postulated by Alsterberg (1927) to explain the distribution of oxygen concentrations, and in particular the very low values sometimes found in the thermocline region. Alsterberg's concepts were in fact the starting point of the treatment given in the present paper. This explanation of the metalimnetic minimum is considered probable by Yoshimura (1939), but Alsterberg's theory cannot be applied to the oxygen of Linsley Pond (cf. Riley, 1940). Alsterberg's whole theoretical position has recently been attacked with considerable vigor by Grote (1936). There is probably much to be said for the position adopted by both investigators; Alsterberg's hydrodynamic scheme (1927, Fig. 6) is certainly an unlikely one, but is not really necessary to a theory of the effect of morphometry on the vertical distribution of dissolved substances. Any series of predominantly horizontal currents would be equally effective. Of all previous investigators, Einsele and Vetter (1938), who have observed very large and rapid changes which they attribute to hypolimnetic water movements in the concentration of iron, phosphorus, silica and other substances in the deeper water of the Schleinsee, perhaps come closer to the position adopted in the present paper. A very brief mention of comparable changes, attributed to water movements, is made by Juday, Birge and Meloche (1938).

THE PHOSPHORUS CYCLE IN LINSLEY POND

THE DATA

3.1.1. The methods used in the determination of phosphorus were those employed by Juday and Birge (1931), oxidation of organic phosphorus being carried out as recommended by Robinson and Kemmerer (1930). Occasionally in the oxidation of total phosphorus the final solution obtained was not as colorless as would be desired, but it is improbable that

any appreciable error has been introduced by this. In determining soluble phosphorus, an effort has been made to read below 0.001 mgrms. per litre. Water-color was at first compensated by Pearsall's (1930) method, using Bismarek Brown; later it was found better to employ the glass screens used in determining the color in a Hellige comparator for this purpose. Owing to the disturbing effect of water color and the difficulty of obtaining perfectly matched and colorless Nessler tubes, it is realized that the determinations of soluble phosphorus at great dilution are not very accurate. When the great variations of total phosphorus summed over the entire lake were first noticed, it seemed possible that some technical source of error was vitiating the experiments, and the need for careful control of the technique was realized. The details of a set of controlled determinations are of sufficient interest to be mentioned briefly. On July 5, 1938, the phosphorus content of the lake was very low, the hypolimnetic values being the lowest ever recorded. A sample of 9 m. water was set aside to be oxidized along with a blank and control of known phosphorus content; all these were oxidized with the series taken a week later. Fortunately one of the greatest rises recorded took place in the interval, the lake gaining over 9 kilos of phosphorus. The 9 m. sample of the previous week gave the correct value (0.004), as did the control (0.010); the blank was completely negative. Since the enormous rise recorded between July 5 and July 12, 1938, was therefore technically above reproach, there is no reason to reject the smaller rises occurring at other times when the control was less rigorous.

3.1.2. Since the main object of the investigation was the construction of a phosphorus balance sheet during stagnation, more attention was given to total phosphorus than to the fractions into which it may be divided. Determinations of *soluble phosphate phosphorus* have, however, been made on occasions at all levels, and in the surface water at very frequent intervals. In the case of the surface water, moreover, determinations of total phosphorus on both unfiltered water and on water after passage through a 35 second membrane filter have been made. The difference between the two determinations is referred to throughout the paper as *sestonic phosphorus*. Subtracting the soluble phosphate phosphorus from the total phosphorus of the membrane filtrate gives the *soluble organic phosphorus*. From the autumn of 1938 to mid-summer of 1939 a series of determinations of soluble phosphate phosphorus in the unfiltered surface water and in a membrane filtrate of the same water has been obtained. The difference between these two determinations, if detectable, gives the amount of *acid-soluble sestonic phosphate phosphorus*. The above scheme of fractionation is identical with that proposed by Ohle (1939); unfortunately his paper and that of Cooper's (1938) were published too late for the technical refinements introduced to be used in the present study.

NATURE AND PROPORTIONS OF THE FORMS OF
PHOSPHORUS PRESENT IN THE
SURFACE WATER

3.2.1. Twenty-three analyses are available of the phosphorus content of the surface waters of Linsley Pond, separated according to the above scheme.

The mean values and standard deviations are set out below:

Seston P 0.0133 mgrms. per litre, $\sigma = 0.0082$
Organic
soluble P ... 0.0060 mgrms. per litre, $\sigma = 0.0036$
Phosphate P .. 0.0017 mgrms. per litre, $\sigma = 0.0019$ ¹⁰

It will be observed that the mean phosphate phosphorus in the surface waters constitutes but 8.1% of the mean total, the organic soluble 28.6%, the mean seston phosphorus 63.3%. The mean total phosphorus, 0.021 mgrms. per litre, is comparable to the figure of 0.023 mgrms. per litre given by Juday and Birge (1931) for the surface waters of 479 lakes in north-eastern Wisconsin. The organic phosphorus of the latter authors corresponds to the sum of the sestonic and organic soluble phosphorus in the present study. The Wisconsin workers found about 88% of their phosphorus in combined form; in the present investigation about 92% is combined in either solid or dissolved form. The general distribution of the phosphorus in the surface waters of Linsley Pond and of the Wisconsin lakes therefore superficially appears to be similar. It is probable that in spite of this superficial resemblance an important difference exists between the distributions of the two mean series. Juday and Birge give five analyses of the phosphorus content of centrifuge plankton; such phosphorus corresponds to the sestonic phosphorus of the present investigation. These five analyses indicate a phosphorus content of from 0.185-0.394% of the dry centrifuge plankton. In the present investigation, with a larger number of observations the comparable determinations range from 0.063-0.775%. Half the Linsley determinations, however, fall into the Wisconsin range; the mean of the five Wisconsin determinations is 0.290%; of the twenty-three Linsley determinations, 0.353%. The two means are clearly closely comparable. If the Linsley sestonic phosphorus be considered as entirely in organic combination and be expressed in terms of the organic seston the latter is found to have a mean phosphorus content of 0.464%. A similar or slightly lower figure may clearly be expected in the case of the Wisconsin lakes. Now according to Birge and Juday (1934) the mean organic sestonic content of these lakes is 1.36 mgrms. per litre. This would therefore correspond to a sestonic phosphorus content of 0.0063 mgrms. per litre, or 27.5% of the mean total phosphorus of the Wisconsin series. The soluble organic would likewise be 0.014 mgrms. per litre or 60.9% of the mean total. It would appear therefore that while in Linsley Pond on an average over 60% of the phosphorus in the epilimnion is in sestonic form, in

the Wisconsin lakes a like proportion is probably in soluble organic form. Juday, Birge, Kemmerer and Robinson (1928) comment on the fact that much of the organic phosphorus present in the Wisconsin lakes appears to be in solution. Both series of analyses contrast markedly with those given for the sea by Redfield, Smith and Ketchum (1937) who find from 70-90% of the phosphorus to be present as phosphate and but 3-6% to be in the seston.

3.2.2. The considerable variation in the phosphorus content of the total seston indicates that factors other than the mere quantity of suspended matter are involved in determining the quantity of sestonic phosphorus. Certain of these factors are amenable to statistical analysis. From twenty-four determinations of sestonic phosphorus (Ps), total seston (Ts), organic seston (Os), seston ash (As) and chlorophyll (C) the following simple correlation coefficients can be computed:

$$r_{Ps.Ts} = 0.560$$

$$r_{Ps.Os} = 0.560$$

$$r_{Ps.C} = 0.527$$

$$r_{Ps.As} = 0.340$$

The first three, being significant to above the 99% level (Fisher, 1934), are regarded as statistically significant, the last is statistically insignificant. The correlation with total seston is not amenable to further analysis. Putting Ps in terms of milligrams per cubic meter to avoid unnecessary zeros, the regression equations corresponding to the second and third correlation coefficients are

$$Ps = 2.81 Os + 5.7 \dots\dots\dots (14)$$

$$Ps = 0.478 C + 6.9 \dots\dots\dots (15)$$

In both equations the independent constant corresponds to almost half the mean sestonic phosphorus; neither can therefore be regarded as very satisfactory expressions of the variation of the phosphorus content with the two variables considered independently. The variation of chlorophyll is, in the present series of observations, largely independent of the variation of organic matter

$$r_{Os.C} = 0.335$$

which is statistically insignificant.¹¹ The partial correlation coefficients

$$r_{PsOs.C} = 0.456$$

$$r_{PsC.Os} = 0.436$$

significant to the 95% level, indicate that a considerable part of the variation of the seston phosphorus with one variable is independent of the variation with the other. The multiple correlation coefficient

$$R_{Ps(C.Os)} = 0.654$$

is a considerable improvement on either simple coefficient. The associated multiple regression equation

$$Ps = 2.07 Os + 0.353 C + 2.7 \dots\dots\dots (16)$$

is likewise an improvement on either of the equations (14) and (15) in that the independent constant is considerably reduced. Figure 19 shows the way in which this equation roughly expresses the major variations in seston phosphorus in 1938-39. Neglect-

¹⁰ Phosphate phosphorus data obviously are not normally distributed, owing to the high autumnal values, which include acid-soluble sestonic phosphate phosphorus.

¹¹ Riley (1939a), using different dates, none of which fell at the height of summer, obtained a significant correlation.

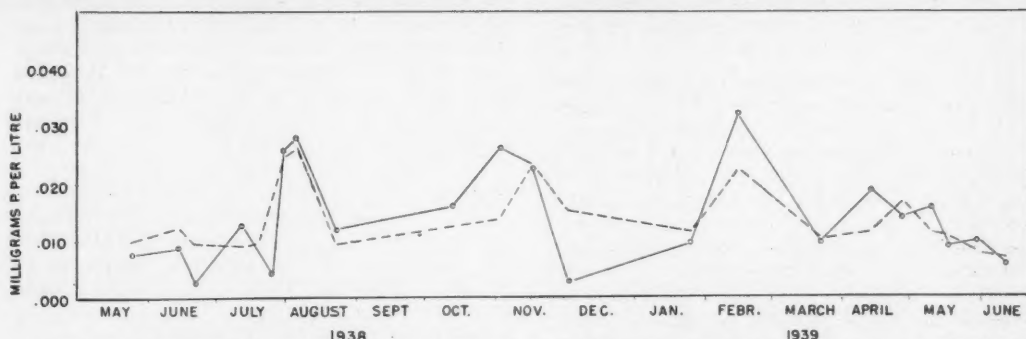


FIG. 19. Variation of seston phosphorus in surface water 1938-1939 observed (solid) and computed (broken) from the multiple regression equation (16).

ing variation due to causes extraneous to either the mass of organic matter or the chlorophyll, and substituting mean values, (16) becomes

$$13.9 = 6.0 + 5.2 + 2.7$$

Very approximately therefore the variations in the phosphorus associated with chlorophyll are as important as variations associated with the whole suspended organic mass. Now since only about 20% of the total organic seston of Linsley Pond is phytoplankton (Riley, 1940), it is clear, for this relation to hold, that the phosphorus content of unit mass of phytoplankton must be greater than that of unit mass of the dead seston or detritus. This conclusion is comparable to that reached by Birge (Birge and Juday, 1934), by more direct methods, relating to the distribution of nitrogen in the planktonic organisms and detritus of the seston.

TOTAL PHOSPHORUS ESTIMATED FOR THE ENTIRE LAKE

3.3.1. From the total phosphorus determinations at individual levels at a station in the center of the lake, the total phosphorus content of the entire lake has been calculated. The mean concentrations of the layers 0-2 m., 2-5 m., 5-7 m., 7-9 m., and 9-11 m. have been taken as the means of the total phosphorus concentrations at the top and bottom of each layer. In the case of the lowest layer, 11-14.8 m., only the 13 m. concentration was used in 1938, the mean of the 12, 13, and 14 m. determinations in 1937. Since there is some reason to believe that the very high values observed in the epilimnion in the latter part of 1938 are due to liberation of abnormal amounts of phosphorus from decomposing algae in the littoral, killed by copper sulphate treatment of the water, the 1937 data will be primarily considered in the analysis of the natural variations in the phosphorus content of the lake. The values for 1938, however, give critical information as to the progress of changes in the hypolimnion. Horizontal variations in all chemical parameters doubtless occur; the experience of most investigators seems to indicate that they are small in lakes of the size of Linsley Pond, and no attempt was made to consider them.

3.3.2. In Figure 20 and Table 11 the estimates of

the total phosphorus content of the lake throughout the thermally stratified period (April to August) in 1937 are presented. The mean of all observations gives a value of 8.98 kilograms of phosphorus in the lake. There is, however, no evidence of constancy of content, nor in this year, of a steady trend either of increase or decrease; the total content rather varies in an irregularly rhythmical manner, from low values of about 6 kilos to high values of about twice that amount. In the earlier part of 1938 similar, and even one more spectacular (3.1.1.), changes occurred; later, after two treatments with copper sulphate, a steady rise took place. Gross technical error having been excluded as an explanation of the observed changes as indicated in 3.1.1., two possibilities present themselves. The increases and decreases might be due to gain of phosphorus through the inlets and loss through the outlet, or it might be due to purely internal changes leading to gain of phosphorus from the mud across the mud water interface, and loss by sedimentation of particles, that had incorporated this phosphorus gained by the free water from the mud. Though the first hypothesis is inherently improbable, as there are cases (Fig. 22) of gains at all levels occur-

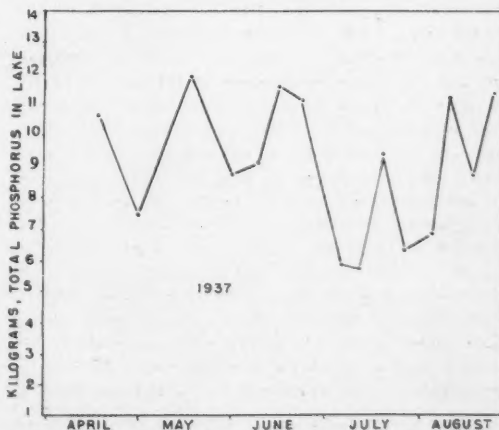


FIG. 20. Linsley Pond. Variation of total phosphorus in the entire lake, 1937.

ring simultaneously under conditions of extreme thermal stratification, when the inlets could hardly affect the hypolimnion, the role of the paralimnion, or environment of the lake, must be considered before an attempt is made to evaluate quantitatively the limnetic or internal changes.

3.3.3. In order to estimate the paralimnetic contribution to the observed changes, estimates of the rate of flow of the two inlets and of the outlet of the lake were made throughout the period of observation, by timing the descent of floating objects in the streams and measuring the mean depth and the width of the streams in the middle of the courses selected. This method is very rough, but the mean flow of the inlets and the outlet, when compared, show that the results must be of the correct order of magnitude. Total phosphorus determinations were made on the same water.

	Water cubic m. per wk.	Total Phosphorus kilos per wk.
Mean income, Inlet 1.....	22,012	0.354
Mean income, Inlet 2.....	5,508	0.118
Total mean income.....	27,520	0.472
Mean loss, outlet.....	24,271	0.365
Net gain	4,289	0.107

The excess of water entering the lake over that leaving would correspond to an excess of 3.4 cms. per week evaporation over precipitation and surface runoff into the lake; this is perhaps excessive and would indicate that the gain in phosphorus, which is very small, is also probably slightly overestimated. If now the individual weekly gains or losses in phosphorus due to the paralimnion are computed from the individual determinations in the waters of the streams, it will be found that they are never commensurate with the observed changes, and that very large residuals due to purely limnetic events are obtained when the gains and losses due to the streams are subtracted from the gains and losses observed in the lake (Table 11).

3.3.4. Differences between successive weeks show that in 1937 net increases of as much as 4.93 kilos per week and net decreases of as much as 3.18 kilos per week, due entirely to limnetic events, are possible; while in 1938 gross increases, in which the inlets can have played but a small part, of 9 kilos per week occurred. In order to obtain at least a minimal estimate of the mean natural rate of replacement, it may, however, be assumed, as a limiting case, that phosphorus only enters the free water from the mud when the total content is rising, only is sedimented when the total content is falling. The net weekly increments when rises are occurring may then be added and divided by the whole time, giving the lowest estimate for the mean rate of regeneration; the net weekly losses when falls are occurring may similarly be added and divided by the whole time giving the minimum estimate for the mean rate of sedimentation. The values so obtained for 1937 are 1.09 kilos per week for the mean gain by regeneration, 0.98 kilos per week for the mean loss by sedimentation. In spite of the fact that these estimates are minimal

TABLE 11 Estimates of gain and loss of total phosphorus from the entire lake. Linsley Pond, 1937.

Date	Kilograms P in Lake	Rate of gain or loss through inlets and outlets	Mean rate of gain or loss between observa- tions	Gross change per week	Net change per week
April 17.	10.60	+0.33	-0.08	-1.65	-1.57
April 30.	7.54	-0.49	-0.19	+2.04	+2.23
May 17.	11.79	+0.11	0.00	-1.98	-1.98
June 1.	7.55	-0.11	-0.06	+0.66	+0.72
June 8.	8.21	(-0.01)	+0.04	+2.33	+2.29
June 15.	10.54	(+0.09)	+0.14	-0.41	-0.55
June 22. (June 29)	10.13	+0.19	-0.06	-2.15	-2.09
July 6.	5.86	+0.64	+0.43	-0.07	-0.50
July 13.	5.79	+0.22	+0.22	+3.49	+3.27
July 20.	9.28	+0.21	+0.20	-2.98	-3.18
July 27.	6.30	+0.18	+0.10	+0.60	+0.50
Aug. 3.	6.90	+0.02	+0.22	+5.15	+4.93
Aug. 10.	12.05	+0.42	+0.23	-2.28	-2.51
Aug. 17.	9.77	+0.04	-0.09	+2.05	+2.74
Aug. 24.	12.42	-0.21			

they are surprisingly high, implying that the average sojourn of a phosphorus atom in the lake, acted on solely by internal forces, is two months, or that during the entire period of the investigation in 1937 phosphorus was entering and leaving the water to and from the mud fast enough to give two entire replacements of the mean amount of the element present in the water. Actually, owing to the nature of the assumptions involved, it is certain that the time of sojourn must be shorter and the rate of replacement more rapid; events in those individual weeks, when 4 to 9 kilos are lost or gained, suggest that phosphorus metabolism of the lake may actually be four to nine times as rapid as the minimum estimate. The mean minimum estimate corresponds to a mean increase of 0.0011 mgrms. per litre, or approximately 0.001 mgrms. per cm^2 of lake surface, which may be regarded as a sufficiently accurate estimate for the mud surface. The maximum increase observed in 1937 (Aug. 3-10) of 5.15 kilos similarly corresponds to an output of about 0.0035 mgrms. per cm^2 of mud; the maximum in 1938 (July 5-12) of 9.78 (gross) to about 0.007 mgrms. per cm^2 mud surface.

PHASES OF STAGNATION

3.4. Except in so far as the epilimnetic values at the end of the summer may be unduly high, there is nothing to indicate that the vertical distribution of phosphorus in the summer of 1938 is abnormal; the data of both years are therefore used in the present discussion. In order to clarify the relations of phosphorus compounds to other substances, and particularly to emphasize the very important relationship, discovered by Einsele (1936, 1938) between the distribution of phosphorus and iron, it has been found

convenient to divide the processes during stagnation at any depth into three phases as follows:

Phase I. The oxygen content falls from the high values of the spring turn-over to about 1 or 2 milligrams per litre; alkalinity starts rising as the oxygen falls; total phosphorus remains low, under 0.03 mgrms. per litre; iron has not been determined but is undoubtedly low.

Phase II. The oxygen content remains low, usually between 1 and 2 mgrms. per litre; alkalinity continues to rise; phosphorus (under 0.03 mgrms. per litre) and iron (under 0.50 mgrms. per litre) low, as in phase I. Manganese, however, may be high.

Phase III. Oxygen content as in phase II or slightly lower; alkalinity rising, but more slowly than in the previous phase; phosphorus and iron rising, ultimately reaching values in excess of 0.10 mgrms. per litre and 5.0 mgrms. per litre respectively.

The essential difference between the first two phases lies in the establishment of a relatively constant low oxygen concentration in phase II; the essential difference between phase II and phase III lies in the rapid rise in phosphorus and iron in phase III. In the first two phases it may be assumed that the redox

potential (irreversible oxygen electrode) is of the order of 0.45-0.50 volt; in phase III it may fall to 0.15 volt (Hutchinson, Deevey and Wollack, 1939). The high iron content of water of any level in phase III is primarily, sometimes exclusively, due to ferrous iron, while the phosphorus is largely present as soluble phosphate (e.g., at the end of August 1938 from 60 to 70% of the total phosphorus is present as soluble phosphate in the bottom layers) in marked contrast to the condition in the well-aerated surface water where the soluble phosphate represents but a small fraction of the total. As Einsele has pointed out, most of the soluble phosphate accumulating in the final phase of stagnation will be precipitated out as ferric phosphate when the ferrous iron is oxidized at the turn-over. The events as they affect one particular level (9 m.) are presented graphically in Figure 21.

VERTICAL DISTRIBUTION OF PHOSPHORUS

3.5.1. Typical distributions for four dates in 1937 are given in Figure 22; more detailed distributions for 1938 in Figures 24-30. In May all depths may be regarded as in phase I. During June and July

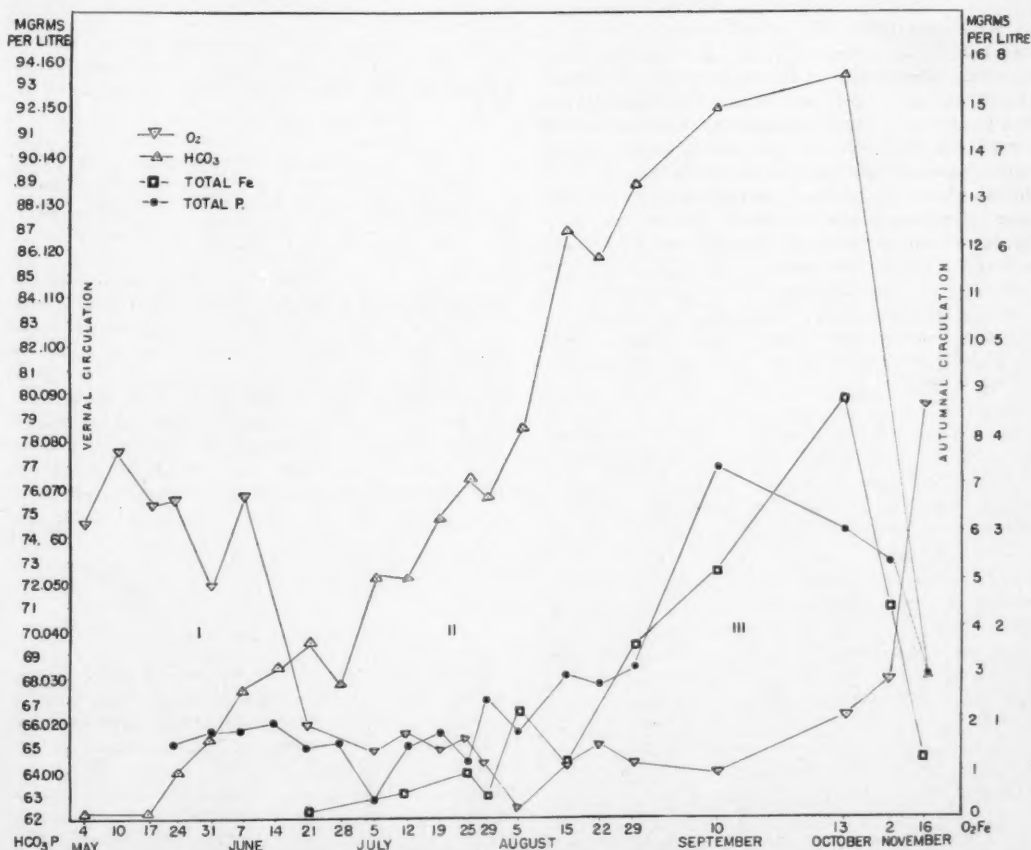


FIG. 21. Linsley Pond. Variation of oxygen, bicarbonate, total phosphorus and iron throughout stagnation in 1938 at 9 m.

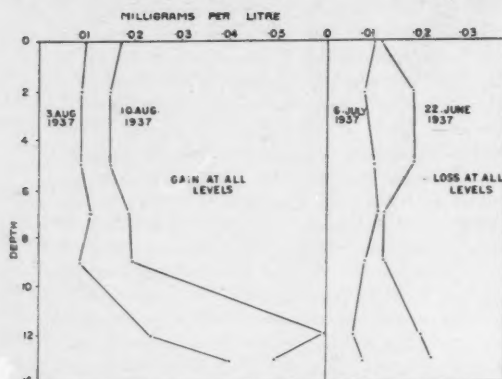


FIG. 22. Linsley Pond. Gain or loss of total phosphorus at all levels between successive determinations in 1937.

the 13 m. water may be regarded as entering phase III, while the rest of the hypolimnion is in phase II. Late in August the 11 and 13 m. levels show phase III fully developed, the 7 and 9 m. levels are still in phase II, the 5 m. level is entering the latter phase. In September phase III is well developed at 9 m., and poorly developed at 7 m. The epilimnion of course is permanently in the early stages of phase I. It is important to note that although great and irregular variations in total phosphorus occur at all depths throughout all phases of stagnation, giving rise to the variations in the total content of the lake discussed in 3.2, there is no tendency to develop any characteristic pattern in the vertical distribution of total phosphorus so long as levels in phases I and II are considered. This is strikingly shown in Figure 23, in

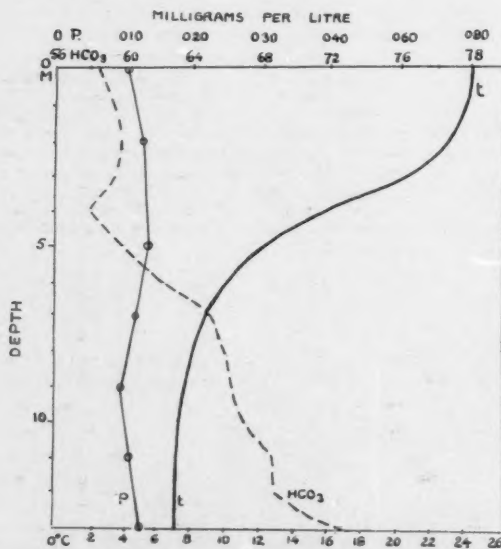


FIG. 23. Linsley Pond. Mean total phosphorus and alkalinity, May 24-July 27, 1937.

which the mean values for the period May 24-July 27, 1937, are presented graphically. During the period in question very considerable changes in the total phosphorus had occurred at all levels, yet the mean curve shows a practically uniform vertical distribution, in marked contrast to the mean alkalinity curve for the same period in which the step-like pattern is already well developed.

3.5.2. Owing to the fact that access of air during filtration precipitates soluble phosphorus in the presence of ferrous salts as ferric phosphate, reliable data for the deeper water could not be obtained (filtration at a low pH might be possible but has not yet been tried). Moreover, it is probable that in the presence of abundant soluble phosphate, even if appreciable amounts of ferrous iron are not present, the filtration

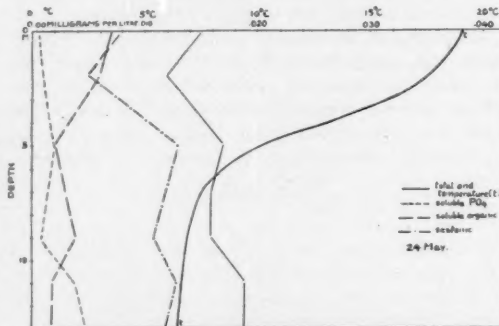


FIG. 24. Linsley Pond. Temperature curve (solid, marked t), total phosphorus (solid), sestonic phosphorus (chain), soluble organic phosphorus (long broken line), and soluble phosphate phosphorus (short broken line) for May 24, 1938.

technique is unsatisfactory owing to adsorption. Nevertheless, a sufficient number of vertical series have been obtained indicating the general nature of the vertical distribution. These series can best be presented in graphical form (Figs. 24-30). Early in the season soluble phosphorus is detectable throughout the lake, and may increase slightly at the bottom. In the latter part of the summer, when all the bottom water is in phase III, practically no soluble phosphorus can be detected in the surface waters but

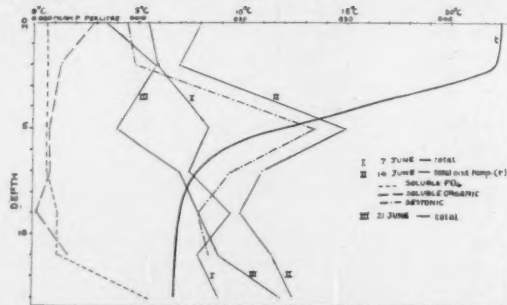


FIG. 25. Linsley Pond. Total phosphorus for June 7 (I), June 14 (II), June 21 (III), and other data for June 14, indicated as in Figure 24. Note the great loss of phosphorus, at 5 m. between June 14 and 21.

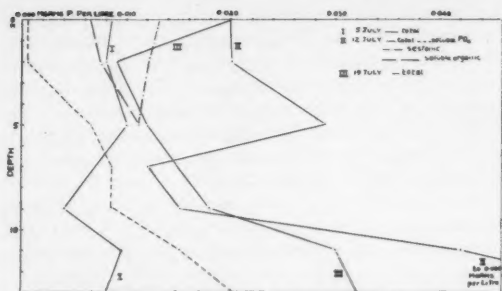


FIG. 26. Linsley Pond. Total phosphorus for July 5 (I), July 12 (II), and July 19 (III), other data for July 12, indicated as in Figure 24.

very large amounts are present in the deeper layers of the lake (Fig. 28). The appearance of soluble phosphorus in the hypolimnion is, however, irregular and temporary establishment of phase III at 13 m. is clearly possible, with a subsequent reversal to phase II as between July 19 and 25 when a loss of soluble phosphate, an increase in total phosphate, and a slight rise in iron occurred. In so far as it has been determined, organic soluble phosphorus is more regularly distributed than the other fractions, though on July 12 it is largely responsible for the peak at 5 m. In general the great irregularities that the total curve may exhibit are largely due to the sestonic fraction.

3.5.3. Owing to the rapid variations exhibited by the phosphorus content, no quantitative treatment comparable to that used in analysis of the variations of bicarbonate content is possible. A rough approach to the problem may, however, be made. In Figure 23 the difference between the mean of the three analyses made in the period May 31-June 15 and the last three analyses made in each season (August 10, 17, 24 in 1937; August 29, September 16 and October 13 in 1938) is given. In spite of the great variation in phosphorus content in the upper seven meters throughout the summer, the only significant effect of prolonged stagnation is to increase the phosphorus concentration of the extreme lower layers of the lake. It is therefore reasonable to suppose that while the

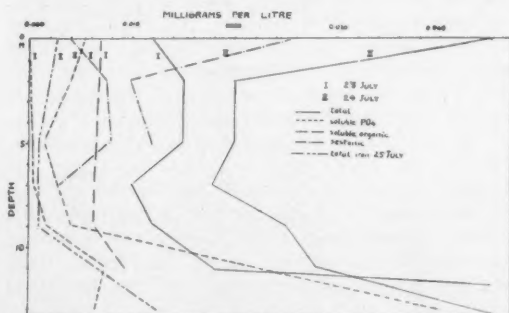


FIG. 27. Linsley Pond. Total, sestonic, soluble organic and soluble phosphate phosphorus for July 25 (I) and July 29 (II), indicated as in Figure 24. Note the enormous increase in sestonic phosphorus at the surface.

regenerative process is dependent primarily on the horizontal current system deduced to explain the observed rates of increase of alkalinity, the cycle proceeds in the epilimnion and the upper part of the hypolimnion in a different way to that in the deepest water. The chemical aspects of this difference have been elucidated by Einsele and are discussed in 3.6.1., but a possible mechanical aspect of the process must be mentioned. Reference to Figures 29 and 30 will show that phase III, though feebly indicated at 7 m., is never properly developed above 9 m. The great increases in phosphorus are confined to the region demarcated as the bathylimnion in the treatment of temperature in 1.2.1. If the speculative interpretation of this region given in 1.10.3. and 2.3.4. be accepted, it seems reasonable to interpret the rise in total phosphorus and total iron in general, and of phosphate and ferrous iron in particular, as due to the effect of density currents carrying a considerable amount of the water present in this region over the highly reductive mud in the depths of the lake. The chemical significance of this process will be clear from the discussion given in 3.6.1.

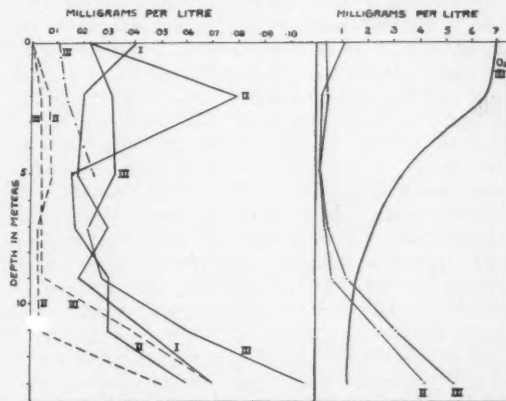


FIG. 28. Linsley Pond. On left, total phosphorus for August 5 (I), August 15 (II), and August 22 (III) and soluble phosphate phosphorus for the second and third of these dates, indicated as in Figure 24, but with the horizontal scale reduced to one fifth. On right, total iron for the second and third date and oxygen for August 22. Note the persistence of the stratification of July 29 through August 5, and the subsequent appearance of immense amounts of non-phosphate phosphorus at 2 m. on August 15.

3.5.4. In the epilimnion and in the first two phases of stagnation in the hypolimnion, rapid removal of phosphorus is needed to complete the cycle. The only mechanisms by which phosphorus can be removed from the water of the lake as a whole are the gravitational sedimentation of seston, and the accumulation of seston on aquatic plants in the littoral. The work of Chandler (1937), on the removal of plankton by the vegetation of rivers, suggests that the second of these mechanisms may be effective in the freely circulating epilimnion, but the gravitational sedimentation of seston is doubtless far more important. On account of the high proportion of

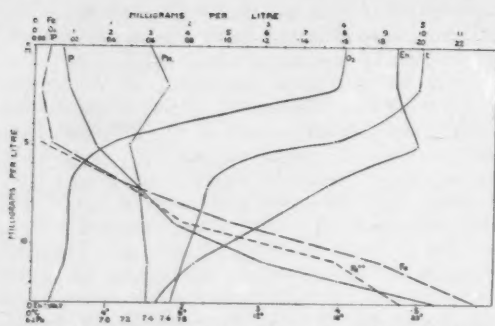


FIG. 29. Temperature (solid, *t*), total phosphorus (solid, *P*), oxidation-reduction potential (solid, *Eh*), oxygen (solid, *O*₂), total iron (long broken lines), and ferrous iron (short broken lines) for September 16, 1938.

sestonic phosphorus in Linsley, as much as half the mean number of phosphorus atoms may be undergoing sedimentation at any time, but with varying speeds depending on the density and size of the sestonic particles involved. Direct evidence of such sedimentation is not indicated in many of the series. The best instance is provided by the fate of the immense amount of phosphorus that appeared in the *Anabaena* bloom between July 25 and 29. This persisted in the surface water at least until August 5, in spite of the treatment of the lake with copper sulphate on July 30. By August 15, the phosphorus content of the surface layer was more normal but a huge accumulation was found at two meters, presumably in detritus formed as the result of the death of the bloom. A week later, on August 22, a somewhat abnormal amount appeared at five meters, though the two-meter level was still high. By September 17 the five- and seven-meter layers were both high, but the significance of the rise at that latter level is uncertain as the phosphorus concentration increases regularly with depth. It is clear that the descent of the phosphorus observed at this time was much slower than is normal; presumably the density of the detritus involved was abnormally low. In the case of the most remarkable reduction in phosphorus content observed, the loss of 0.022 mgrms. per litre at five meters between June 14 and 21, 90% of the

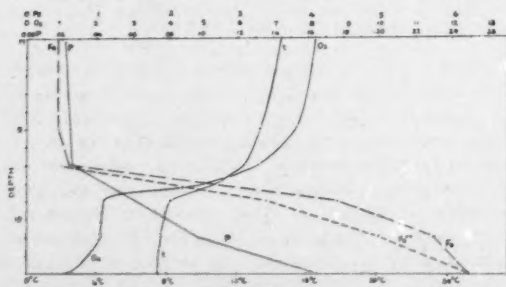


FIG. 30. Linsley Pond. Temperature (solid, *t*), total phosphorus (solid, *P*), oxygen (solid, *O*₂), total iron (long broken lines), and ferrous iron (short broken lines) for October 13, 1938.

phosphorus was present in sestonic form at the level in question on the first date. There is no evidence of the reappearance of any of this phosphorus at a lower level on the succeeding visit; losses in fact occurred at all levels. A very large amount of the seston at five meters had therefore apparently fallen to the bottom of the lake or at least below 13 m. in a week. Such a descent implies a rate of fall of 1.14 m. per day, i.e., 4.75 cms. per hour or 0.8 mm. per minute. This seems rather rapid but may well be possible. A somewhat similar but less extensive diminution was observed between July 12 and 19, also at five meters. Here 0.017 mgrms. per litre was lost and in this case only 0.011 mgrms. of sestonic phosphorus was initially present, so part of the rather large amount of soluble (phosphate 0.007, organic

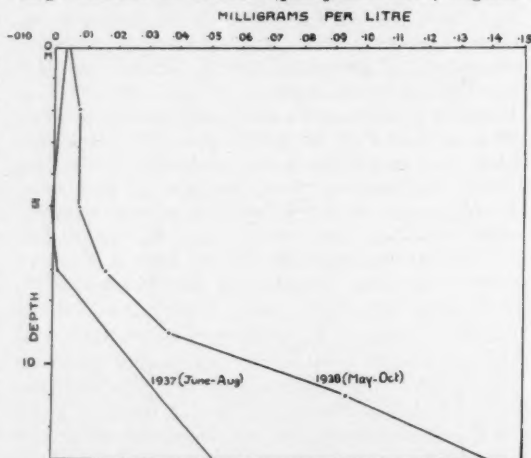


FIG. 31. Linsley Pond. Increment in total phosphorus, at the levels analyzed, occurring between the first three and last three analyses of each season.

soluble 0.011) phosphorus must have been absorbed before sedimentation could occur. There is, however, in this case some indication of a part of the phosphorus reappearing at 7 and 9 m. where rises of 0.003 mgrms. per litre occurred. It is obvious that without a knowledge of the thickness of the band of high concentration initially indicated at five meters, no further analysis is possible. In general, however, it would appear that the only possible mechanism that could produce sedimentation of the magnitude implied by the observed variations is the concentration of detritus and nannoplankton into faecal pellets as the result of the feeding activities of the zooplankton.¹² Such pellets might well have the density and magnitude required to cause the observed changes. Dr. Riley kindly informs me that the phytoplankton (mostly minute green algae) volume at five meters, on June 14, was 0.418 cm³ per m³, on June 21, 0.438 cm³ per m³, the zooplankton on the first date 0.569

¹² Since the above was written, J. Grim (Int. Rev. Hydrobiol. 39: 193-315, 1939) published data on the rate of loss of diatoms through death and sedimentation in Lake Constance which indicate that the figure given above of 1.14 m. per day is by no means impossibly high even if the material is not concentrated in faecal pellets.

cm^3 per m^3 and on the second, 0.448 cm^3 per m^3 . An excess in favor of zooplankton in the P:Z ratio is unusual in the lake and may well explain the very great drop at 5 m. on the period involved. By very indirect means Dr. Riley computes that at least 23.5% of the phytoplankton produced at the 5 m. level was eaten between the dates in question. As replacement is fairly rapid this may represent a considerable faeces production. The percentage of phosphorus in the seston would inevitably fall in such a process, but data do not exist to prosecute this phase of the analysis further.

COMPARISON WITH OTHER LAKES

3.6.1. Six sets of determinations of total phosphorus in Lake Quassapaug, made during the summer of 1938, show similar but less rapid changes. The greatest rise took place between July 1 and 15 (Fig. 32) when the total phosphorus of the entire lake increased from 48 kilos to 77 kilos. A slight increase to 92 kilos occurred during the next two weeks, followed by a slow fall throughout August. The rate of output during the maximum rise was about $0.0013 \text{ mgrms. per cm}^2$ per week, contrasting with the high values of $0.0035\text{--}0.007$ observed on occasions in Linsley Pond, and very little above the minimum mean estimate for the latter locality. The low rate of output of the mud of Lake Quassapaug, even

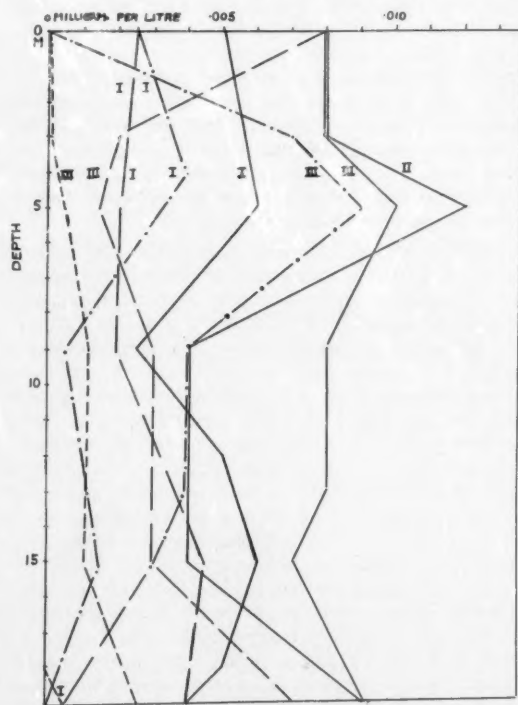


FIG. 32. Lake Quassapaug. Total phosphorus for July 1 (I), July 15 (II), August 11 (III), 1938; sestonic, organic soluble and soluble phosphate phosphorus for the first and third dates. The fractions are indicated as in Figure 24.

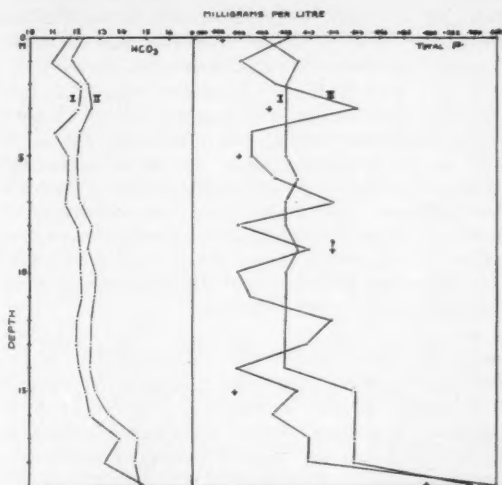


FIG. 33. Lake Quassapaug. Total phosphorus (right) and alkalinity (left) for August 18 and August 25, 1938. Crosses indicate soluble phosphorus determinations for the second date; that at 9 m. is, however, clearly erroneous. Note the extraordinary stratification that developed in the lake.

at times of relatively rapid rise, is in keeping with the oligotrophic character of the lake. The last two series of determinations, on August 18 and 25 respectively, present a curious problem (Fig. 32). An effort was made to determine total phosphorus at one meter intervals throughout the whole depth of the lake. The first set, obtained on August 18, show a normal distribution, with a slight increase near the bottom of the lake. On August 25, however, although the total content of the lake had changed but little, the total phosphorus had become distributed in a series of bands, reminiscent of the narrow strata often encountered in plankton studies, or of the optical stratification described by Whitney (1937, 1938). A few soluble phosphate determinations show that a considerable amount of the phosphorus is in ionic form; unfortunately at 9 m. there is an excess of soluble over total phosphorus in the recorded figures. This error tends to cast doubt on the whole series, but it is difficult to see how an error presumably increasing the soluble phosphorus, i.e., some contamination, would decrease the total phosphorus at certain levels, as is undoubtedly indicated by the curve for August 25 when compared with conditions a week earlier. The fact that total phosphorus in the lake has changed but little would also favor acceptance of the second series; it is not improbable that the error at 9 m. concerns only this single soluble sample. If the analyses be reliable, they indicate a remarkable transport of phosphorus from one layer to another, and its rapid regeneration *in situ* in the layer to which it is brought. Such an occurrence is presumably possible in a lake in which there is a large amount of zooplankton performing vertical movements and but little phytoplankton, rapid regeneration being known in sea water when zooplankton is

decaying (Cooper, 1935). The ratio of zooplankton to phytoplankton is certainly higher in Lake Quassapaug than in the majority of the lakes of Connecticut.

3.6.2. Juday, Birge, Kemmerer and Robinson (1928) give three series of analyses for Trout Lake which exhibit fluctuations very similar to those occurring in the Connecticut lakes. The table showing the organic phosphorus given by Einsele and Vetter for the Schleinsee (1938) also gives clear indications of a rise of about 25% in the total phosphorus content above 9 m. between August 6 and August 19, 1935. Too little data have been published by other workers to permit further comparisons.

RELATIONSHIP OF IRON AND PHOSPHORUS

3.7.1. Einsele (1936, 1938) has made very important studies of the relationship of iron and phosphorus. His main results can be summarized as follows: When a solution of ferrous bicarbonate containing a soluble phosphate is oxidized by aeration, ferric phosphate and ferric hydroxide are precipitated; the phosphate separates before the hydroxide, so that if phosphate is present in excess no hydroxide is formed. The hypolimnetic waters of most eutrophic lakes are rich in both ferrous iron and in phosphate, but the former is usually in excess so that when such waters are aerated ferric hydroxide containing a greater or less amount of phosphate is precipitated. This happens at times of overturn, when a precipitate of ferric hydroxide and ferric phosphate is distributed throughout the lake. In a few weeks this precipitate settles, so that the greater part of the hypolimnetic phosphorus cannot enter into biological circulation. Since iron is precipitated as phosphate before hydroxide is formed, partial oxidation will remove phosphorus and iron differentially, the water being depleted of the former before the latter is wholly removed. This may happen if turbulent mixing occurs in the upper part of the hypolimnion, giving a ratio of Fe:P that decreases with depth. Einsele's further experiments indicate that CO_2 and reducing substances, particularly H_2S , must be considered. If H_2S is added in increasing amounts to a suspension of ferric hydroxide and phosphate in the presence of CO_2 and the absence of oxygen, at first both ferrous bicarbonate and phosphate go into solution, but, with the addition of increasing amounts of the reducing agent, ferrous sulphide is precipitated, leaving the phosphate in solution. It is probable that the conditions in the mud resemble the final state of such an experiment; if the water in contact with the mud is rich in oxygen and a brown oxidative microzone is formed, the conditions in the microzone are to be compared with the initial conditions of the experiment and no phosphate can leave the mud. If, however, the oxygen is reduced in the water, as in phase II of stagnation according to the terminology of the present paper, a time will come when the oxidative microzone will disappear and conditions at the mud-water interface will resemble those of the middle phase of the experiment when ferrous iron goes into solution as bicarbonate and phosphate. In

Linsley Pond, in the mud of which there is an excess of iron over sulphur (Hutchinson and Wollack, 1940) the final condition of Einsele's experiment cannot be realized; reducing substances other than hydrogen sulphide are presumably involved and there is little if any possibility of loss of iron as sulphide in the free water as a final phase in stagnation. It is clear that the ferrous-ferric system is acting in Einsele's experiments as a poisoning system. Interesting studies could be made by measurement of redox potential in the hypolimnia of lakes rich in decomposing organic matter but relatively poor in iron. Finally Einsele has made a study of the effect of colloidal ferric oxide in adsorbing phosphate from solution. Under the usual conditions found in nature it would appear that, although this process takes place, it is quantitatively unimportant.

3.7.2. The distribution of iron and phosphorus at the end of the summer in Linsley Pond is essentially the same as that found by Einsele, though the absolute amounts of phosphorus are smaller than in the Schleinsee and Stadtsee, and the increase in the phosphorus relative to the iron with increasing depth is less regular than in the two German localities. The data, set out graphically in Figures 29-31, indicate the similarity of the stratification observed in Linsley Pond and in Einsele's localities; while the concomitant increases in iron and phosphorus at 9 m. (Fig. 21) demonstrate the working of Einsele's principle at a single depth most clearly. Some sedimentation of phosphorus doubtless occurs in phase III, but the essential difference between this phase and the previous one must be in the enormous increase in the rate of diffusion of phosphate from the mud once the limitation imposed by the presence of oxidizing ferrous iron in the microzone is removed. Such a condition is likely first to develop in profile-bound density currents if such currents occur.

3.7.3. Although Einsele found that the greater part of the ferric compounds produced in suspension by oxidation of ferrous iron at times of circulation were sedimented in a week or two, it was observed in the present investigation that appreciable amounts of ferric iron are normally present in suspension in Linsley Pond. It seemed possible, therefore, that part of the phosphate normally determined as soluble, might really be in a suspended but acid-soluble form. Accordingly a series of determinations was made of the soluble phosphate in both unfiltered water and in membrane filtrates, from a 35 second membrane filter which retains all solid particles of diameter over c. 0.5μ . Differences of the order of 0.0002 mgrms. per litre, which are barely detectable, are probably due to differences in the color of filtered and unfiltered water, and are insignificant. The results, set out in Table 12, indicate that only at the time of the autumnal turn-over is any appreciable amount of suspended acid-soluble phosphate present. This may be regarded as ferric phosphate. In Linsley Pond, where the pH is normally between 7 and 8 and the calcium content is but moderately high, the occurrence of calcium triphosphate, recently discussed by

Gessner (1939), need not be considered. While the results confirm Einsele's conclusions as regards the fate of the phosphate at the time of turn-over, there is a strong possibility that some of this suspended phosphorus may be used by the phytoplankton, as Harvey (1937) has shown that suspended ferric compounds can be utilized by marine diatoms.

3.7.4. Although ferric phosphate is now known not to be a normal constituent of the seston ash, the supposed occurrence of free ferrous iron, presumably undergoing oxidation, in both the sea (Cooper, 1932) and in the surface waters of lakes (Hutchinson, Deevey and Wollack, 1939) suggested that possibly part of the control of the phosphorus content of the lake might be a hydrometabolic precipitation by iron which supposedly reached the free water from the mud in a reduced state, and when oxidized combined with phosphate present in solution. Although the results of a further study of the matter indicate that the presence of free ferrous iron in the epilimnion is probably an illusion, due to the dipyriddy method of determination, the details of this study, while not strictly relevant to the phosphorus cycle, are of sufficient interest to warrant mention. Aliquots from two samples, A, the untreated water, and B, a membrane filtrate from a 35 sec. filter, were analyzed in the following ways:

- (1) Ferric iron, without oxidation or other treatment.
- (2) Apparent ferrous iron, by dipyriddy (some reduction of ferric occurs).
- (3) Reducible iron by dipyriddy and sodium sulphite.
- (4) Total iron after evaporation, gentle ignition solution and reduction, by dipyriddy.

It is thus possible to determine

- (a) Total iron in seston (A4-B4) and in solution (B4).
- (b) Ferric iron in seston (A1-B1) and in solution (B1).

TABLE 12. Phosphate phosphorus and iron in the surface waters of Linsley Pond, November 1938-June 1939.

Date	Temp.	Sol. P. Unfiltered	Sol. P. Filtered	Acid-sol. seston P.	Total seston P.	Total Fe.	Ferric seston Fe.
1938							
Nov. 2...	11.9	0.0037	—	—	—	0.27	—
Nov. 16...	10.3	0.0052	—	prob. present	—	0.43	—
Dec. 2...	1.2	0.0065	0.0039	0.0016	0.003	—	—
Dec. 5...	—	0.0091	0.0073	0.0018	—	0.55	0.14
1939							
Jan. ...25...	2.91	0.0021	0.0021	0.0000	0.010	0.28	0.03
Feb. 15...	3.2	0.0008	0.0008	0.0000	0.032	0.16	—
March 22...	—	0.0022	0.0021	(0.0001)	0.010	0.30	0.04
April 5...	7.8	0.0023	0.0022	(0.0001)	—	0.10	0.05
April 13...	7.5	0.0020	0.0020	0.0000	0.019	—	—
April 27...	13.2	0.0009	0.0009	0.0000	0.014	0.07	0.03
May 10...	17.7	0.0015	0.0017	(-0.0002)	0.009	0.10	0.03
May 24...	16.2	0.0009	0.0008	(0.0001)	—	—	0.03
May 30...	—	0.0006	0.0006	0.0000	0.010	—	—
June 13...	24.1	0.0003	0.0003	0.0000	0.010	—	—
June 23...	24.0	0.0004	0.0004	0.0000	—	—	—
June 29...	24.3	0.0004	0.0004	0.0000	—	—	—

- (c) Ferrous iron in seston (A3-B3)-(A1-B1) and in solution (B3-B1), which may be instructively compared with the total apparent ferrous iron (A2).

- (d) Combined iron, presumably organic, in seston (A4-B4)-(A3-B3) and in solution (B4-B3).

The color of the water makes readings below 0.01 mgrms. per litre impossible; tripyridyl, which is more sensitive, could not be obtained. No dipyriddy being commercially available during the end of 1938 and beginning of 1939 it was not possible to make complete fractionations before March, 1939. During May, 1939, some substance, destroyed on ignition and presumably organic, developed in the seston which gave a brownish color in the presence of sodium sulphite and dipyriddy, at the same time decreasing the intensity of the red co-ordination compound formed with ferrous iron. Procedure three was therefore not possible on unfiltered water after the end of April, and the number of analyses is therefore very limited; the results are set out in Table 13. Some data on ferric iron were obtained in the fall of 1938 and are incorporated in Table 12. Ferric iron appears

TABLE 13

Date	Total iron		Ferric iron		Ferrous iron		Organic iron	
	sest.	sol.	sest.	sol.	sest.	sol.	sest.	sol.
Mar. 1(frozen)	0.150	0.03	0.030	0.000	0.01	0.00	0.035	0.11
Mar. 22(ice breaking)	0.250	0.05	0.040	0.000	0.04	tr. ≤ 0.01	0.07	0.18
Apr. 5(open)	0.070	0.03	0.050	0.000	0.02	tr. ≤ 0.01	0.07	0.01
Apr. 28(open)	0.040	0.03	0.030	0.000	0.01	0.00	0.03	0.00(4)
May 17(open)	0.080	0.025	0.030	0.00	—	0.00	0.01	—
Mean March-April.....	0.130	0.035	0.040	0.000	0.02	<0.005	0.075	0.03

to be a normal constituent in suspension; in view of Harvey's (1937) observations, it may well be the main source of iron in the nutrition of the phytoplankton. Table 12 shows an abnormal quantity present after autumnal circulation, as found by Einsele. As is to be expected, no ferric iron appears in solution; doubtful traces were found in one incomplete analysis, May 29, 1939 (Table 12), when some suspended hydroxide may have passed the filter. Unequivocal evidence of ferrous iron in solution is also not forthcoming; on the two occasions on which traces are reported ferrous iron is high in the seston and traces may have passed the filter which does not retain colloidal material. The absence of detectable amounts of ferrous and ferric iron in ionic solution is to be expected since Cooper (1937) finds theoretically that at pH 7.0 on attainment of equilibrium not more than 4×10^{-8} mgrms. per litre of iron in true solution, mostly as ferrous and FeOH^{++} ions, is present. The occurrence of ferrous iron in suspension at the time of the breaking of the ice and of the vernal circulation seems to be well established; on the other two dates the amounts recorded, being obtained by difference, are not significant. The high figures for apparent ferrous iron should be contrasted

with those obtained by difference, and clearly indicate the impossibility of using dipyriddy in the estimation of small amounts of ferrous iron in the presence of suspended ferric hydroxide, owing to the continual removal of ferrous ions from solution in the formation of the red co-ordination compound and the consequent destruction of the original equilibrium (Harvey, 1937). No significant difference between the apparent ferrous and the reducible iron of the membrane filtrates was ever detected. The high values for ferrous iron in surface waters given by Hutchinson, Deevey and Wollaek are due to a failure to realize this limitation of the method. In the first two analyses the large amounts of suspended combined iron may well be present in the form of complexes derived from soils and brought into the lake by melt water running under the ice. The hardly detectible amounts present on later dates probably represent the normal iron content of the organisms of the plankton and their derivatives. Significant amounts of combined iron occur in solution on all dates.

PHOSPHORUS AND NITROGEN AS LIMITING FACTORS

3.8.1. In a later paper it is hoped to discuss the significance of the ratio of nitrate to phosphate, in its relation to the qualitative changes in the plankton of Linsley Pond. A few notes on other aspects of the interrelation of the cycles of these elements may not be out of place in the present contribution. The first aspect to be considered is the role of the two elements as limiting factors. Riley (1940), studying the matter statistically, found a significant correlation between the nitrate and the phosphate content of the surface water and the quantity of phytoplankton present a week later; he concluded that phosphate was the more important limiting factor, but the data were not extensive enough to permit final judgment. The matter has been also examined experimentally in a series of experiments in collaboration with Dr. Riley. In these experiments, bottles holding approximately 3.5 litres were filled with surface water and suspended to a frame or buoy, so that they hung

under water at the surface of the lake. Potassium phosphate or potassium nitrate was added in solution in quantities to raise the phosphorus or nitrogen by 1 mgrm. per litre to two bottles; both nutrients were added to a third bottle, a volume of distilled water equal to that of the solutions, to a fourth control bottle. The chlorophyll content of the water in the bottles after thorough mixing was determined after a week's exposure in the lake, the content in the nutrient bottles being compared with both the control and with the initial and final content in the lake. In discussing these experiments it is necessary to separate from those done during the spring and early summer, two performed when much *Anabaena* was present, the behavior of the latter organisms being (3.7.2) clearly atypical. The results of four experiments done before an *Anabaena* bloom appeared are presented in Table 14. It is obvious that little change occurred in the control bottle, while addition of nutrients singly, produced some increase in the phytoplankton. This increase, however, is small compared to that effected when both nutrients are added together. The results suggest that on the whole nitrate is somewhat more significant than phosphate in producing an increase, but that both elements must be present before any other possible limitation can come into play. The possibility that some potassium must be added to obtain the full result is unfortunately not excluded by these experiments, though the effect of this element is clearly small. As far as they go the observations recorded in the table suggest that the results obtained may well depend on the qualitative composition of the phytoplankton at the time under consideration. A considerable increase in the phytoplankton would undoubtedly occur if an accession of both elements were to occur simultaneously, but it is possible that the bloom so produced would shade the water below, and so would not greatly increase the productivity of the whole lake (Riley, 1940).

3.8.2. Unlike the phosphorus cycle, the nitrogen cycle is to some extent open to the atmosphere; the significance of nitrogen-fixing bacteria has long been

TABLE 14

Period	Initial Nitrate Nitrogen mgrms. per litre	Initial Phosphate Phosphorus mgrms. per litre	Initial Chlorophyll mgrms. m ³	Control		1 mgrm. of P per litre added			1 mgrm. of N per litre added			1 mgrm. of P and 1 mgrm. of N per litre added			Final Chlorophyll in Lake Surface	
				Chlorophyll	Percent of Initial	Chlorophyll	Percent of Initial	Percent of Control	Chlorophyll	Percent of Initial	Percent of Control	Chlorophyll	Percent of Initial	Percent of Control	Chlorophyll	Percent of Initial
Year 1937																
April 30-May 7.	c. 0.02	0.001	14.2	13.2	93.2	15.3	108	116	18.7	132	142	99.4	702	754	12.7	89.5
May 17-May 24.	0.022	0.001	7.5	5.5	71.8	11.1	148	207	7.7	102	143	49.7	665	927	8.0	107.0
June 15-June 22.	0.019	0.0005	6.8	5.9	87.0	8.4	125	143	16.5	243	279	79.2	1163	1343	4.8	70.2
July 13-July 20.	0.030	0.000	9.6	9.9	105.5	14.5	154	146	29.8	312	296	206	2165	2062	9.2	96.3
Mean of Percentages...	89.4	134	146	197	215	925	1272	90.8

considered in limnological literature; in small eutrophic lakes, the nitrogen-fixing capacity of the alga *Anabaena*, recently established by De (1939, Fritch and De, 1938) may be as important as an annually recurring source of nitrogen in the lake. In 1938 a few determinations of total (Kjeldahl) nitrogen in the surface water, before and after filtration through No. 42 Whatman paper, were made during the rise of the *Anabaena* bloom. The final determination was made on a bottle of water suspended for a week after the *Anabaena* had been killed in the lake by copper sulphate treatment. This bottle showed a huge increase in phytoplankton, practically all *Anabaena*, over the previous week, the saponifiable ether-soluble green pigments rising from 25.6 mgrms. per cubic meter of chlorophyll to 65.6 mgrms. per cubic meter. A very great increase in the combined nitrogen present is also to be observed. Although the Linsley water was presumably not bacteria-free, and the *Anabaena* present in the lake was *A. circinalis* (Francis Drouet det.), a species not among the three studied by De, there can be very little doubt that the intense nitrogen fixation observed was due to this alga.¹³ The data obtained in this way are presented in Table 15.

TABLE 15

Date	Total Organic N. Mgms.	Soluble Organic N. per litre	Chlorophyll	Remarks
19 June	0.54	—	8.0	Little <i>Anabaena</i>
25 June	0.79	0.51	20.3	Water-bloom
29 June	1.00	0.92	25.6	Bloom decaying
5 Aug.	1.98	1.11	65.6	In bottle, healthy bloom

A curious condition is exemplified by the *Anabaena* in the bottle exposed between June 29 and August 5, which has also been noticed on other occasions. The bottle when filled contained a great deal of decaying *Anabaena* filaments; the nitrogen figures suggest that much of the organic material of these filaments had been liberated in soluble form. During the week of exposure in the bottle a very great development of the bloom occurred, producing a chlorophyll content higher than has ever been observed in the lake. In an experiment done in 1937 with nitrogen and phosphorus, a very similar condition was noted, the chlorophyll in the control bottle rising from 34.5 on August 31 to 98.7 on September 7; in none of the experimental bottles was there a comparable rise. In some of Dr. Riley's experiments on oxygen production in clear bottles at the lake-surface in September, 1937, a similar rise in the number of *Anabaena* filaments was obvious, at a time when they had almost disappeared from the lake. These observations clearly throw little light on the nature of the phenomenon, but suggest that the growth of *Anabaena* is facilitated either by the non-turbulent state of the water in a

full stoppered bottle or by some substance produced, bacterially or otherwise, at the glass-water interface. The effect is so striking that it deserves further investigation; it clearly invalidates all conclusions in nutrient experiments at the time when a bloom is at its height or early decline.

3.8.3. Finally a few words may be added on the ratio of combined phosphorus and nitrogen in the seston and in solution. So few observations are available that if they were not concordant with the deduced experience of other investigators they would not be worth mentioning. An unknown source of ammonia, probably from a leaking gas outlet, vitiated the Kjeldahl determinations made at the end of the investigation to add to the evidence assembled. The following figures appear to be reliable.

Date	Seston N.	Seston P.	Sol. org. N.	Sol. org. P.
5 April	0.17	0.016	0.256	0.0021
27 April	0.14	0.014	0.359	0.0016
17 May	0.23	0.009	0.406	0.008

The ratio of the nitrogen to phosphorus in the three seston determinations lies between 9.4:1 and 25.5:1; in marine planktonic organisms, Cooper (1938a) considers a ratio of 15:1 in milligram atoms or 6.8:1 in milligrams as typical. The three values given above are all greater than this, the lower two are of the same order of magnitude. On the other hand, the soluble combined nitrogen bears a ratio to the soluble combined phosphorus of from 50:1 to 220:1. The ratio of total combined nitrogen, other than nitrate, to the total non-phosphate phosphorus lies between 23:1 and 37:1. In the Wisconsin lakes the mean total combined nitrogen is .457, the mean non-phosphate phosphorus (organic of Juday and Birge) is .0203, the ratio being 22.5:1. The soluble organic phosphorus appears on an average to be higher than in Linsley Pond; if the estimate given in 3.2.1. be correct, the ratio is 27.1:1. Similarly the ratio of sestonic nitrogen to sestonic phosphorus in Wisconsin appears to be about 14:1. These figures strongly suggest that organic nitrogen is liberated in inorganic form less easily during the decomposition of planktonic organisms than is organic phosphorus. Birge (in Birge and Juday, 1934) moreover has shown that a comparable situation exists with respect to nitrogen and carbon. It is therefore very probable that in general, phosphorus is liberated more easily than nitrogen, nitrogen more easily than carbon, in the regeneration of inorganic substances from organic in aquatic environments.

HORIZONTAL CURRENTS AS A GENERAL FACTOR IN LIMNETIC INTERMEDIARY METABOLISM

3.9. The two factors primarily responsible for the rise in the bicarbonate content of the hypolimnion are the pelometabolism of the mud, which causes the production of bicarbonate in the first instance, and the horizontal water movements by which the material is carried into the free water. There can be no possible path by which phosphorus is carried rapidly, at all levels of the hypolimnion, into the central part of the lake other than the same water movements. In

¹³ Since the above was written, an entry in *Chemical Abstracts* (33: 5446, 1939) has brought to my attention the observations of B. S. Aleev and K. A. Mudretsova (*Microbiology* (U. S. S. R.) 6: 329-338, 1937). These investigators, whose original paper I have not seen, apparently observed similar phenomena in a pond during the period of water-bloom; unfortunately no indication is given, in the abstract, of the nature of the alga believed by them to be a fixer of nitrogen.

the epilimnion, where the mode of indirect treatment adopted in the present paper is inapplicable, the relative importance of horizontal movements and turbulent exchange between water in immediate contact with mud in the littoral region, and the surface layers immediately above the contact water, cannot be estimated. All the energy required to produce the horizontal and turbulent movements induced in the first and second part of the paper must have originally been delivered at the surface. Much of this energy is certainly dissipated in the epilimnion, and it is safe to conclude that if a change involving transport from the mud can be demonstrated in the hypolimnion, *a fortiori*, it is mechanically, though not necessarily chemically, possible in the epilimnion. It has been adequately demonstrated that increases in total phosphorus can occur at all levels in phases I and II of stagnation, when chemical conditions are essentially epilimnetic so far as this substance is concerned. The dilemma resulting from the work of Juday and Birge therefore is resolved, for in all trophogenic layers a continual replacement is possible by the same mechanism that results in the rise in the bicarbonate content. The special conditions found at the bottom of the lake, producing the full development of phase III, may well be due not only to absence of illumination, but also to the supposed system of density currents which would have given the water finally appearing well away from the bottom, for example at 11 m. in the center of the lake, unusual opportunity to be influenced by the surface layer of the mud. The general theoretical scheme implied in the present paper is represented diagrammatically in Figure 34. The mechanisms of this scheme can be invoked in general, to explain all observed rises in concentration, in any of the substances dissolved in the lake. It is equally clear that the internal metabolic cycle of every different substance

will have specific characteristics, which though unintelligible without a knowledge of water movements, require specific biochemical treatment. The phosphorus cycle may be considered as one of the simplest of such specific cycles.

THE PHOSPHORUS CYCLE AS A SPECIFIC EXAMPLE OF INTERMEDIARY METABOLISM

3.10.1. The phosphorus cycle in Linsley Pond may be characterized by certain general properties, which are probably not exhibited together by the cycle of any other ordinary eyelical element.

(a) It is ideally a *closed cycle*. In an ideal abstraction no exchanges need occur between the lake and the paralimnion in phosphorus metabolism. In practice some small amount of phosphorus is brought into the lake by the inlets in excess of that lost through the outlet, and this excess presumably compensates for what is lost to the sediments of the lake. Over short periods of time there is *no need to consider such replacements as inevitable parts of the cycle*, which, in broad outline, can be understood without reference to anything but the events in the water and the mud with which it is in contact.

(b) The cycle is intimately bound up with the biocenosis of the lake, and is of such a nature that at any one time a *very high proportion of the element present in the water is in particulate organic form*. This means that during a part of the cycle most of the quantity of the element present comes under the influence of gravity, so leading to greater removal by sedimentation than would be exhibited by an element such as nitrogen, in organic combination, where a large part of the atoms are present in soluble, or at least colloidal, forms which have a negligible tendency to sediment.

(c) *The rate of regeneration from the mud varies with the redox potential of the layer into which the regenerated phosphorus is entering, or more probably is dependent on the redox potential at the mud-water interface of this layer. This dependence, however, is not direct, but depends on the relationship of phosphorus and iron.*

3.10.2. The significance of these characteristics can best be made clear by reference to certain other elements. The nitrogen cycle in the biosphere has been described *ad nauseam*, but in any given biotope is frequently inadequately understood. Cooper's (1937a) theoretical treatment for the sea may be profitably consulted, as a more modern presentation of the most complex known elementary cycle than is usually given in textbooks. Such information as is available for lakes indicates very clearly that (a) the cycle is open to the atmosphere; (b) although the element is as important biologically as is phosphorus, its fate in the free water is probably quantitatively different, as a greater proportion of the nitrogen in lake waters appears to be present in soluble organic form, at least when comparison is made in a given lake or district; (c) the dependence on redox potential is clearly very marked and iron may be involved, but the effects of variations of the potential are

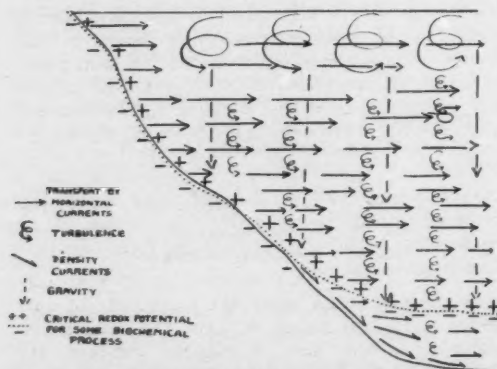


FIG. 34. Diagrammatic representation of the path of dissolved substances (not water-movements in general) passing from the mud into the free water according to the theory developed in the present paper (solid lines) and of the path (broken) of sedimenting substances whose concentration is non-conservative in the free water (i.e., phosphorus). The dotted line separating - from + signs indicates the boundary between redox potentials critical for the occurrence of some process that accelerates the loss of the solute from the mud.

largely mediated by bacterial action and are probably more qualitative (ammonification versus nitrification) than quantitative (Mortimer, 1939).

3.10.3. Riley has considered the copper cycle in Linsley Pond. Here there is a strong presumption in favor of an essentially open cycle, but one in which the inlets rather than the atmosphere are involved. The behavior of copper in relation to the proximate fractions of organic matter in the free water is curiously similar to that of phosphorus, and abundant opportunity for sedimentation occurs. The association, however, is probably a process of adsorption, rather than entry into the metabolic cycles of individual organisms. The vertical distribution of copper in full stagnation shows a far less marked maximum at the bottom than is found in the case of phosphorus (Riley, 1939a) so that the redox potential is probably not involved either directly or indirectly.

3.10.4. It is highly probable that the types of criteria used in 3.10.1. to characterize the phosphorus cycle could be used to classify elementary cycles in any aquatic biotope. A somewhat more general form of each criterion could be introduced. The importance of the direction in which the cycle is open, if at all, needs no emphasis. The second criterion, when generalized, relates to the effect of chemical and biological events on the direction of migration of the element. The effect of the biochemical properties of an element on its mobility must be considered with care; Yoshimura finds that sodium behaves in most lakes as a non-biological element, in spite of its great physiological importance. The third criterion, that of the conditions under which the simple inorganic compounds, capable of biological utilization, are liberated and accumulate need not be limited to a discussion of redox potential. It is, however, probable that the relative state of oxidation or reduction of a portion of an environment is of more general significance than many investigators have realized. In order to emphasize the great importance of this aspect of the elementary cycles, reference may be made to the recent work of Oparin (1938) for a discussion of the occurrence of free oxygen, carbon dioxide, and nitrogen in the earth's atmosphere. Evidence exists that points to the conclusion that the original condition of the earth's biosphere was one of general reduction. Some corollaries of this conclusion have been considered by Oparin with respect to the oxygen, carbon and nitrogen cycles. The significance of the hypothesis with respect to other biological elements, notably iron, phosphorus and calcium, remains to be elucidated. If speculations of the sort so ingeniously developed by Oparin have any validity, it is probable that biogeochemical studies of parts of the biosphere with low oxidation-reduction potentials may throw unexpected light on the early history of living beings.

SUMMARY

1. A study of the rate of change of temperature with respect to time, in Linsley Pond, North Bran-

ford, Conn., Lake Quassapaug, Middlebury, Conn., and in Lake Mendota from Birge's table of mean temperatures, indicates that thermally the hypolimnion can be divided into an upper *clinolimnion* in which the rate of heating falls exponentially with increasing depth, and a lower *bathylimnion* in which the rate of heating approaches a constant value independent of depth.

2. In the *clinolimnion*, the coefficient of turbulence can be calculated, using McEwen's method. For the mean temperatures and rates at the height of stagnation values of 0.86 m.² per month, for Linsley Pond, 6.55 m.² per month for Lake Mendota and about 1.1 m.² per month for Lake Quassapaug are obtained.

3. McEwen's detailed procedure, in which bathylinnetic values of the rate of change of temperature with respect to depth are used, is criticized, as not fulfilling his own condition for a constant value of the coefficient of turbulence. McEwen's values of the coefficient of turbulence in Lake Mendota are therefore too high, and the residuals obtained in the hypolimnion and explained by his statistical theory of convectional cooling appear to be unreal.

4. There is no evidence of a vertical variation of turbulence in inverse relationship to stability in the *clinolimnia* of any of the lakes studied.

5. In Lake Mendota, turbulence decreases with increasing stability throughout the heating season.

6. Application of the first and second order equations of Schmidt to determine the coefficient of turbulence in the *bathylimnion* leads to conflicting results. The conflict can only be resolved by supposing that the *bathylimnion* heats by some mechanism other than vertical turbulence. There is reason to believe that there is little change in the value of the coefficient of turbulence in passing from the *clinolimnion* to the *bathylimnion*.

7. If the total heat income at any level is calculated on a Birgean basis, the first and second order equations give reasonably consistent results in the *clinolimnion*. This means that some of the heat passing into the *bathylimnion* has previously passed through part of a horizontal plane in the *clinolimnion* lateral to the contour describing the top of the *bathylimnion*.

8. It is suggested that heating by profile-bound chemical density currents is largely responsible for the formation of the *bathylimnion*. Heating by biological oxidations is entirely inadequate.

9. The use of Grote's regional modulus of turbulence suggests that while the coefficients of turbulence of the *clinolimnia* of Lake Quassapaug and Linsley Pond are not significantly different, the epilimnion of the former lake is about four times as turbulent as that of the latter.

10. The morphometric relationship observed in the mean curve relating bicarbonate content to depth in Linsley Pond during summer stagnation, previously reported for 1937, is shown in its essential features by the 1938 data.

11. From the results of the study of temperature and turbulence, it is possible to determine what part of

the observed rate of increase of bicarbonate is due to vertical mixing and what part to other water movements. The latter are of much greater importance than turbulent vertical mixing. The relationship observed between morphometry and the bicarbonate curve shows that such other water movements are primarily horizontal currents, but a consistent scheme emerges if the supposed density current mechanism is taken into account.

12. The metabolism of the hypolimnion of a stratified lake may be regarded as composed of *hydro-metabolism* or the series of chemical cycles taking place in the free water, and of *pelometabolism*, or the sum of chemical cycles occurring in the mud or at the mud-water interface, in so far as they affect the free water. In Linsley Pond the pelometabolism appears to constitute about 20% of the total metabolism estimated in terms of carbon dioxide production.

13. In the surface waters of Linsley Pond there is a slight excess of calcium and magnesium over bicarbonate. In the deep water of the hypolimnion, there is a considerable deficiency of calcium and magnesium, made up by ammonium and ferrous ions. Iron and magnesium appear to increase regularly with depth; calcium may show transitory maxima in the upper part of the hypolimnion; rapid and extensive variations in the manganese content of the hypolimnion and in the mode of stratification of this element were observed.

14. On an average, the phosphorus content of the surface waters of Linsley Pond is divided into soluble phosphate phosphorus, 8%, soluble organic phosphorus, 29%, and sestonic organic phosphorus, 63%. The proportion of sestonic phosphorus is probably unusually high.

15. The variations in sestonic phosphorus are correlated with both the mass of organic seston and the quantity of phytoplankton, as measured by its chlorophyll content. The phytoplankton probably contains more phosphorus per unit mass than does the detritus of the seston.

16. Acid soluble sestonic phosphate (ferric phosphate) is only present in the surface waters after the autumnal overturn.

17. Variations in the total phosphorus content of the whole lake are considerable and rapid. In the summer of 1937, the lake gained on an average at least 1.09 kilograms per week, and lost on an average at least 0.98 kilograms per week, independent of gain and loss through the inlets and outlet. The actual rate of replacement may be 4 to 9 times as great as this minimum estimate.

18. Variations can occur at all depths and can only be interpreted in terms of horizontal water movements that carry phosphorus from the mud-water interface into the free water, and of continual sedimentation of the considerable fraction present as sestonic phosphorus. It is suggested that faeces production by the zooplankton constitutes the chief sedimenting agency.

19. Comparable, but less rapid, variations in the total mass of phosphorus present in Lake Quassa-

paug are recorded; similar changes are deduced from data published by other investigators.

20. It is convenient to divide the processes of stagnation at any depth into three phases. In phase I oxygen falls rapidly, while bicarbonate begins to rise. In phase II there is a relatively constant low oxygen content, with rising alkalinity; iron and phosphorus are both low. In phase III the oxygen remains low while bicarbonate increases, though less rapidly; ferrous iron and soluble phosphate phosphorus increase rapidly.

21. Einsele's work on the resulting vertical distribution of iron and phosphorus is confirmed, and is of great significance. The limitation of the accumulation of phosphate in the presence of high oxygen concentrations is briefly discussed in relation to oxidation-reduction potentials and the ferrous-ferric poisoning system.

22. In the surface waters of Linsley Pond ferric iron is normally present in suspension but not in solution; ferrous iron may apparently sometimes be present in suspension, but not in solution; organic iron is present in variable amounts in suspension and in rather constant amounts in solution. It is suggested that suspended ferric hydroxide may be a source of iron available to phytoplankton.

23. Addition of a mixture of potassium phosphate (K_2HPO_4) and potassium nitrate to surface water suspended in a bottle in the lake leads to a great increase in the phytoplankton over that present in a control bottle. Addition of one or the other salt alone leads to a smaller increase, sometimes greater in the nitrate than in the phosphate bottle and sometimes the reverse. When an *Anabaena* bloom is present the results are irregular, mere isolation of the alga in a bottle of lake water appears to favor its multiplication.

24. Evidence is presented that the nitrogen-fixing capacity of *Anabaena*, recently established by De, is of importance in the metabolic cycle of a lake containing appreciable quantities of the alga.

25. The phosphorus cycle is characterized by being ideally closed, by being dependent on the gravitational sedimentation of organisms or their excreta, and by being indirectly dependent on the oxidation-reduction potential. Characterization of other elementary cycles by the use of similar criteria is possible.

26. The oxidation-reduction potential of environments is significant in general biological theory in view of the probable prevalence of highly reduced substances throughout the biosphere in the early history of the earth.

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VEGETATION OF ROAN MOUNTAIN: A PHYTOSOCIOLOGICAL
AND SUCCESSIONAL STUDY

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	63	Grassy Bald Community	79
THE AREA	63	Rhododendron Bald Community	82
Location	63	Alder Bald Community	85
Topography	63	SUCCESSION	87
Geological History	63	Beech-Maple Community	87
Soils	64	Spruce-Fir Community	87
Climate	64	Balds	88
Vegetational History	65	Grassy Bald Community	88
TERMINOLOGY	67	Rhododendron Bald Community	90
METHODS	67	Alder Bald Community	91
VEGETATION	68	HISTORICAL VIEWS BEARING UPON BALD	
Beech-Maple Community	69	SUCCESSION	92
Spruce-Fir Community	74	DISCUSSION	94
Bald Communities	79	SUMMARY	96
		LITERATURE CITED	97



An area in which three major plant communities of Roan Mountain meet: northern hardwood forest, northern coniferous forest, and "subalpine" grassy bald. Looking eastward from a point immediately northwest of Carvers Gap.

VEGETATION OF ROAN MOUNTAIN: A PHYTOSOCIOLOGICAL AND SUCCESSIONAL STUDY¹

INTRODUCTION

On cool, moist summits of the higher Southern Appalachians there exists a vegetation more like that of the northeastern United States and Canada than of the surrounding country. Roan Mountain, located in the midst of these southern mountains and rising more than 4,000 feet above the country about it, presents a unique condition to anyone interested in its vegetation. For more than a century it has been considered by many people to be the most beautiful and interesting mountain east of the Rockies, and thus has attracted botanists from both this country and abroad. André Michaux, who was sent to this country by France, was perhaps the first white man to explore the mountain. He was soon followed by such men as Nuttall, the younger Michaux (son of André Michaux), Fraser, Gray, Curtiss, Sargent, Harshberger, Scribner, Lamson, Small, Heller, and others including present-day botanists. Earlier botanists were primarily interested in systematic studies rather than the sociological aspects of the vegetation.

This study represents observations of the vegetation on Roan Mountain which have been made at intervals from 1926 to the present. A detailed survey of the vegetation was begun in 1934 and continued during the summers of 1936 and 1937.

American ecologists have, in the past, been chiefly concerned in determining vegetational changes while Europeans have, in the main, been content merely to present a static picture of the vegetation. No study of the vegetation is complete that does not take into account both its structural and developmental aspects. The aim of this study was twofold. First, it was desired to obtain an adequate description of the present vegetation of Roan Mountain, and second, to consider the dynamics of the vegetation in reference to time and space. The first was accomplished by making a detailed statistical study of the various plant communities within the area, while the second was determined by several lines of evidence relative to successional trends of the communities under consideration.

Since there lie within the area under study the most beautiful and most easily accessible mountain areas of rhododendron in the country, such a study should prove of practical value in formulating a future conservational policy for these natural gardens, whether they be under private or public control. It should also prove of interest to ecologists in that it supplies data from an unusual portion of the Southern Appalachians.

The writer wishes to acknowledge his indebtedness to Dr. H. J. Oosting for advice and criticism throughout the study; to Dr. S. A. Cain for advice pertaining to the statistical surveys; to his wife, Thelma, for help in collection and preservation of plants and for clerical assistance; and to those who helped in tax-

onomic matters. The writer, however, assumes responsibility for any errors which may be present.

THE AREA

LOCATION

The Southern Appalachians may be divided into two major mountain masses, the Unaka Mountains to the west and the Blue Ridge Mountains to the east, each of which extends northeasterly. Southward from the Unakas, trending toward the Blue Ridge, extend various cross ranges of which Roan is the highest. It is located along the northern portion of the North Carolina-Tennessee state line at latitude 36° west and longitude 82° north. An automobile road extends from the town of Roan Mountain, Tennessee, some 12 miles to the summit. The area of Roan Mountain proper is about 12 square miles, but if the total area represented by the entire mountain mass is considered, the area is approximately 50 square miles.

TOPOGRAPHY

The Roan Mountain mass rises from a broad base of about 2,500 feet altitude to a rounded summit of 6,285 feet. The area in Tennessee is drained by the Doe River while the area in North Carolina is drained by the Toe River, both of which flow into the Tennessee River. The summit of Roan forms a broad and rounded divide about 5 miles in extent along the state line, ranging from an altitude of 5,500 feet at Carvers Gap to 6,285 feet at Roan High Knob. Many rounded spurs extend on either side of this divide, alternating with broad "V" shaped valleys. Details of topography are shown in Figure 1.

GEOLOGICAL HISTORY

The rock formations are Pre-Cambrian, being igneous and metamorphic rocks of the Archean and consisting of Roan gneiss and Cranberry granite (Keith, 1907). Gneiss caps the mountain and is underlain by granite.

The history of the area may well have begun with the formation of Carolina gneiss, oldest known formation of the Appalachian province. This was followed by uplift and volcanic action in the Archean when the Roan gneiss cut through the Carolina gneiss in great dykes and formed thin sheets over the latter. Base-leveling and submergence in early Cambrian times was followed by four great cycles of sedimentation which ended with the close of the Carboniferous when a great uplift stopped deposition. A long period of erosion followed, which, by the end of the Cretaceous, had reduced the province to nearly a featureless peneplain, the Cumberland or Cretaceous

¹ A thesis submitted in partial fulfillment of requirements for the degree of Doctor of Philosophy in the Graduate School of Arts and Sciences of Duke University, 1938.

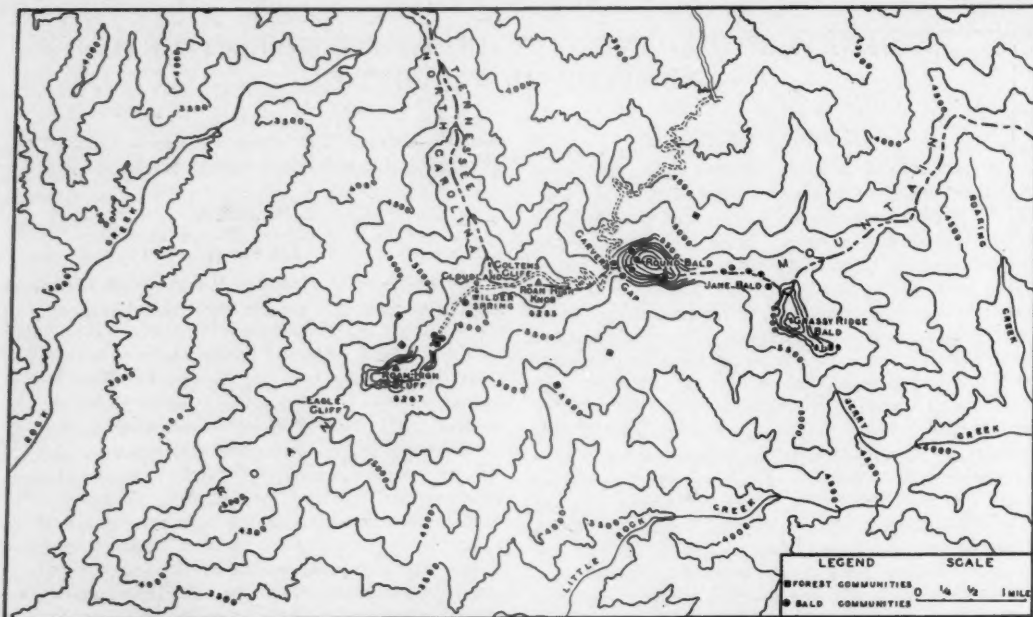


FIG. 1. Map of summit of Roan Mountain showing major portion of the area under investigation. (Based on U. S. Geol. Survey, North Carolina-Tennessee, Bakersville, and Carvers Gap Quadrangles, 1934.)

penneplain. A final uplift of the region resulted in a warped surface and an irregular topography. Since this last uplift, erosion has greatly affected the peaks and ridges, resulting in the rounded present-day appearance.

SOILS

Marbut (1935) has shown the area as belonging to the Gray-Brown Podsolie Soils, but no soil survey has yet been made. Parent material of the summit, and that extending down the slopes to about 4,000 feet, is Roan gneiss composed chiefly of hornblende, gneiss, and schist, with a little diorite. Based on Marbut's soil map (1935) and the writer's limited observation while studying the vegetation, the soils appear to belong to the Chester series which is characterized by a parent material of ancient crystalline origin producing a yellowish or grayish C horizon upon decay.

Soils of forested slopes are fertile, rocky to sandy, loams with medium to high acidity and poorly developed profiles. They vary in depth from a few inches over large boulders and rock outcrops to several feet in the lower coves. Soils of gently rolling balds vary from a thin, gray, gravelly mineral material an inch or so thick to a black fertile loam 1 to 3 feet deep. More than 95 percent of the soil surface of both forest and balds is covered with vegetation.

CLIMATE

Climate of the Southern Appalachians in general is characterized by a lower temperature, greater precipitation, and higher wind velocity than the surrounding country. Available weather data for the

area under study are confined to a three-year precipitation record and to some brief notes kept at camp during the summers of 1934 and 1936 with regard to temperature, showers, and relative amounts of sunshine. Precipitation data were obtained by a self-recording rain gauge established on Cloudland January 3, 1935, by the Tennessee Valley Authority. Data from a 30-year record at Banner Elk, North Carolina, were used since its climate more nearly approaches that of the area under study than any other United States Weather Bureau station in the region. Banner Elk is located about 15 miles eastward on a high rolling plateau at 3,750 feet altitude. Data are also presented from a 23-year record at Johnson City, Tennessee, since it is the second closest station with a continuous record. This station is located about 18 miles northward at an altitude of 1,575 feet. Mean monthly temperature and precipitation for the stations outside the area are presented in Figures 2 and 3, while mean weekly and monthly precipitation for the summit of Roan Mountain is shown in Figure 4.

TEMPERATURE

The annual mean for Johnson City is 57.1° F. while that for Banner Elk is 51.4° F. By interpolation, based on altitudinal differences, the mean annual temperature for Cloudland would be about 44° F. The highest temperature record in 30 years for Banner Elk was 95° F. in July and the lowest temperature was -21° F. in December, an extreme range of 116° F. while the mean monthly range was 33.2° F. Edson (1894) reports -30° F. as the lowest temperature on Roan Mountain for the winters 1892 and 1893. The

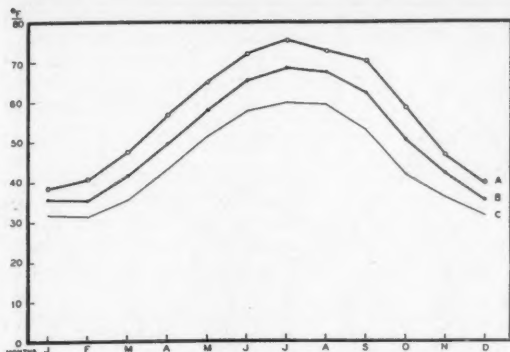


FIGURE 2

FIG. 2. Mean monthly temperatures of two nearby U. S. Weather Bureau stations. The mean monthly temperatures for Johnson City, Tennessee, are based on a 20-year period (1911-1930) while those for Banner Elk are based on a 30-year period (1908-1937).

A. Mean monthly temperatures for Johnson City, Tennessee.

B. Mean monthly temperatures for Banner Elk, North Carolina.

C. Mean monthly temperature predicted for Roan Mountain, North Carolina-Tennessee.

lowest July temperature for Banner Elk was 35° F., an extreme range of 60° F. for July, although the mean range was only 21.9° F. The average frostless season for Banner Elk is 147 days, the shortest reported for North Carolina, but it varies from 87 to 178 days. Since Roan Mountain rises 2,535 feet above the station at Banner Elk it has greater extremes in temperature and a shorter growing season, as would be expected.

PRECIPITATION

Mean annual precipitation for Johnson City is 44.39 inches, for Banner Elk 53.62 inches. Mean annual precipitation for Cloudland during 1935, 1936, and 1937 was 55 inches as compared to 60.49 inches at Banner Elk for the same period, a reversal of

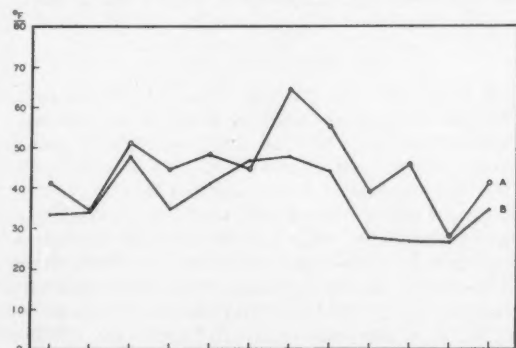


FIGURE 3

FIG. 3. Mean monthly precipitation for Banner Elk (A) and Johnson City (B). Based on a 30-year record (1908-1937) for Banner Elk and a 35-year period (1896-1931) for Johnson City.

what might be expected. Mean annual snowfall at Banner Elk is 39 inches, the second highest in the state of North Carolina. Precipitation for this area is fairly well distributed throughout the year with the lowest monthly mean of 2.78 inches in November and the highest monthly mean of 6.43 inches in July. The highest monthly precipitation on record for Banner Elk was 24.06 inches in July, 1916, and the lowest for the same station was 0.31 inches in August, 1925. Annual precipitation ranges from 36.05 inches in 1925 to 72.95 inches in 1908. For the 3-year period (1935-1937) on Roan Mountain, rain fell each week. The lowest monthly amount was 3.22 inches in June and highest in July, 9.33 inches. There seem to be no dangerously dry periods although there was a nineteen-day period in June, 1936, with only 0.1 inch precipitation which was serious enough to kill as high as 20 percent of the grass clumps in some areas of the grassy bald.

SUNSHINE, CLOUDS, AND FOG

Based on camp records, less than 10 percent of the days of summer have continuous sunshine and less than half of them have as much as 75 percent sunshine. The 3-year record for Cloudland shows that rain fell on about half of the days of summer with July having greatest number of rainy days and June having fewest. Edson (1894), in referring to winter conditions at the summit, says: "The clouds here usually float about level with the summit, though they sometimes rise as much as 500 feet above it, or sink 2,000 feet below; so that it may be said to lie in the track of the clouds." These prevailing conditions gave rise to the name "Cloudland" for the mountain summit.

WIND

In the mountains, the direction of prevailing winds is influenced by general topography of the region. Winds tend to follow courses of the valleys, being deflected by the mountains. The writer's observations for several recent summer seasons indicate that the prevailing winds for most of the area are from the north, coming from the extensive Doe River Valley. Occasionally the wind is from the south, coming from the valley of the Toe. In strongly exposed areas, as in the grassy balds, wind is almost continuous and varies from brisk to strong.

VEGETATIONAL HISTORY OWNERSHIP

The area has been in private ownership since the region was first settled. The largest single tract, containing about 2,700 acres, extends along the mountain summit for a distance of about 5 miles and includes most of the area under study above 5,000 feet altitude. The tract supports essentially all of the spruce-fir forest and heath-bald vegetation on the mountain, most of the grassy and alder balds, and some of the beech-maple vegetation of the upper slopes. Very little land above 4,000 feet has been cleared for cultivation.

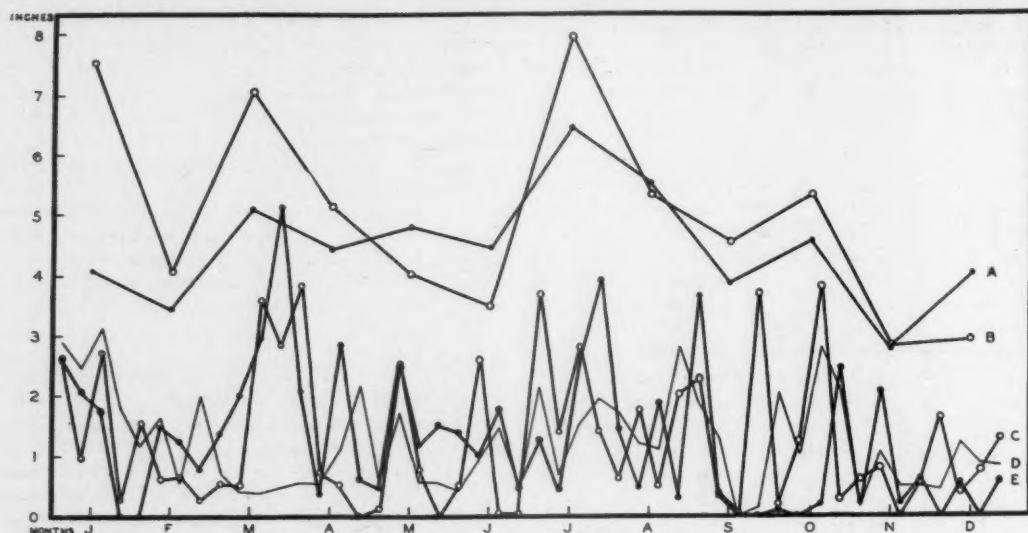


FIG. 4. Mean precipitation on the summit of Roan Mountain by weeks for a three-year period. Based on daily readings as recorded by Tennessee Valley Authority for 1935, 1936, and 1937. Also mean monthly precipitation of Banner Elk and Roan Mountain shown for comparison.

- A. Mean monthly precipitation for Banner Elk.
- B. Mean monthly precipitation for Roan Mountain.
- C. Mean weekly precipitation for Roan Mountain, 1936.
- D. Mean weekly precipitation for Roan Mountain, 1937.
- E. Mean weekly precipitation for Roan Mountain, 1935.

GRAZING

The grassy balds have doubtless been grazed since the days of the first white settlers. Mitchell (1835) described this mountain meadow more than a century ago as the summer pasture ground for young horses of the whole country about it. No attempt was ever made to restrict grazing until the first hotel was built in 1877. A renewed attempt was made in 1936 by the Roan Mountain Scenic Highway Company but the area has been grazed continuously regardless of restrictions. Most of the grazing in recent years has been by cattle and sheep. There is no evidence of overgrazing at present.

LUMBERING

The first major cutting was done from 1883 to 1886 when the cherry of the upper slopes, principally on the south side, was cut. From observations of old stumps and logs, it is evident that some of the larger birch and maple trees were also cut about the same time. The next major cutting was begun in 1929 and finished in 1937. This cutting was very destructive since it removed all sound spruce and fir trees above 6 inches d.b.h. So far as can be determined from human or vegetational records, this was the first major disturbance of the spruce-fir forest, although there had been light local cuttings when two hotels were built, one in 1877 and another in 1884. Fuel for summer use in these hotels was obtained principally from the near-by coniferous forest but was supplemented by some beech from Carvers Gap. Most of the hardwood belt has been cut over lightly from

time to time during the past 50 years. In all except the recent spruce-fir cutting, only the larger trees of the more desirable species were removed.

FIRES

So far as can be learned no forest fires have occurred above 4,000 feet altitude, but the settlers have frequently burned the grassy balds in late fall or early spring to improve grazing. Two mountaineers of the region who are more than 70 years of age told of having seen fires set to the grass periodically for the past 50 years, saying, "mean fo'ks done it." This was confirmed by the presence of ring scars of beech trees at the edge of the grassy balds.

OTHER DISTURBANCES

It is reported that 30 or 40 years ago a train load of rhododendron was shipped north to a botanical garden. Between the years 1927 and 1935 a dozen or more truck loads of this shrub have been removed from the mountain. Many small clumps and canes of rhododendron are removed annually by numerous tourists and natives who visit the rhododendron areas each season. Root and herb collectors have been active in the region for many years, but it appears that they have disturbed the vegetation very little at higher altitudes; however, in 1937 more than a dozen cherry trees were noted which had been cut and stripped of their bark. Early in 1938 many sugar maple saplings on the north slope were also stripped. Least conspicuous but perhaps most significant are effects produced by the local climate. The early

summer drought of 1936 killed about one fourth of the grass clumps on the northern slopes of Round Bald. In spite of minor disturbances, the summit vegetation appears to be in a relatively virgin state except for the recent spruce-fir cutting.

TERMINOLOGY

Terminology used in this study is essentially as defined by Braun-Blanquet (1928). Reference is also made to Cain (1932) who has conveniently summarized fundamental European concepts for American workers. In some instances the original meanings of terms have been slightly modified in order to describe more adequately the points in question. To avoid misunderstanding, the major concepts are here defined in the sense that they are used in this paper.

Community. In spite of the work of the Sixth International Botanical Congress, the "association" concept is not yet standardized. The term "community" is used in this paper primarily in the sense of the "association" as used by Nichols (1929), and Toumey and Korstian (1937). In this study plant communities are characterized by a distinct physiognomy and a definite floristic composition.

Frequency has to do with homogeneity (the uniformity of distribution of species throughout a community) (Braun-Blanquet, 1928, p. 39). It is the ratio of number of quadrats (sample plots) containing a given species to number of quadrats surveyed, expressed as a percentage (frequency index).

The relative homogeneity of stands and communities may be compared graphically by frequency diagrams, provided quadrats of the same size be employed. These diagrams show percentage of species belonging to each frequency class. The five frequency classes here used are as follows:

Class A—species in 0-20 percent of quadrats.

Class B—species in 20-40 percent of quadrats.

Class C—species in 40-60 percent of quadrats.

Class D—species in 60-80 percent of quadrats.

Class E—species in 80-100 percent of quadrats.

Density is the number (abundance) of individuals on a unit area basis. The numbers of individuals recorded from the actual area surveyed were reduced either to a meter or an acre basis.

Cover deals with the surface covered by individuals of each species. The five-point scale of Braun-Blanquet (1928, p. 32) was further subdivided. Class 1 was divided into two classes: Class 0, representing species with less than 1 percent coverage, and Class 1, representing species covering 1 to 5 percent of the surface. This proved very satisfactory since such a large number of species occurred in each community with coverages less than 1 percent. The six-point scale as used in this study follows:

Class 0—species covering less than 1 percent of the ground surface.

Class 1—species covering 1 to 5 percent of the ground surface.

Class 2—species covering 5 to 25 percent of the ground surface.

Class 3—species covering 25 to 50 percent of the ground surface.

Class 4—species covering 50 to 75 percent of the ground surface.

Class 5—species covering 75 to 100 percent of the ground surface.

Basal area is a concept of foresters and is the total cross-sectional area in square feet of the stems of a species based on diameters at 4.5 feet above the ground (d.b.h.). This is a convenient way to show physiological dominance of tree species, since there is probably a close correlation between basal area and the surface or volume of tree crowns.

METHODS

To obtain a clear and accurate picture of the organization of the plant communities of Roan Mountain, reliable analytical data were essential. Such data were obtained by the quadrat method. To obtain adequate data for a quantitative analysis of the vegetation, more than a thousand quadrats were employed. Within individual stands these were randomized somewhat after the Latin square method.

MINIMAL AREA

Since the size of sample plots has been shown by Gleason (1929), Cain (1932, 1934) and others, to affect the concept of frequency, it is desirable to employ a suitable size for each layer of each community. Sizes employed for the forest communities were suggested by Cain (in conference in 1934) based on his experience with similar communities in the Great Smoky Mountains. Due to a marked difference between the physiognomy of the bald communities of Roan Mountain and the Great Smokies, it seemed advisable to determine the minimal area experimentally. This was done according to the method described by Cain (1932). Size of quadrats used in each community and type of data obtained from each are shown in Table 1.

TABLE 1. Sizes of quadrats used for the respective layers of the various communities and kind of data secured from each.

Size (Meters)	Layer	Community	Kind of Data Obtained
1 x 1 ...	Herb and ground	Beach-Maple Spruce-Fir	Coverage by classes; frequency.
1 x 2 ...	Herb and ground	Grassy Bald	Coverage by classes; frequency.
1 x 2 ...	Shrub, herb, and ground	Alder Bald	Density of height classes for woody species; frequency. Coverage by classes for species of each layer; frequency.
2 x 2 ...	Shrub, herb, and ground	Heath Bald	Density by height classes for woody species; frequency. Coverage by classes for species of each layer; frequency.
4 x 4 ...	Shrub	Beach-Maple	Density by height classes; frequency.
5 x 5 ...	Shrub	Spruce-Fir	Density by height classes; frequency.
10 x 10 ...	Tree	Beech-Maple	Density by d.b.h. classes; frequency; stratification estimated.
10 x 20 ...	Tree	Spruce-Fir	Density by d.b.h. classes; frequency; stratification estimated.

In laying out quadrats, compass lines were maintained for control. A steel tape was used for tree and shrub quadrats and standard meter sticks for the other quadrats. The d.b.h. classes of trees were determined with a steel diameter tape. Height classes of woody species were determined by measuring, if less than 6 feet tall, and by estimating, if of greater height. Coverages for species of the herb layer and for the ground layer as a whole were recorded according to the six-point scale previously described.

DISTRIBUTION OF QUADRATS

As shown in Table 1, three kinds of quadrats (herb and ground, shrub, and tree) were employed in forest communities. A base line was first laid out across one end of a stand. Control lines were established at right angles to the base line. Spacing of quadrats along and between control lines was adjusted to size of the stand in order to insure broad sampling and even distribution. Shrub and tree quadrats were usually spaced at 50-meter intervals, each shrub quadrat being located in the corner of the tree quadrat adjacent to control line and nearest base line. Herb quadrats were spaced along control lines at distances one fifth of intervals between tree and shrub quadrats. Only one size of quadrat was employed for each bald community as shown in Table 1. These quadrats were distributed in the same manner as were the herb quadrats of forest communities. Corners of each stand were marked with wooden stakes or pieces of 0.5 inch painted iron pipe.

Quadrat data concerning the spruce-fir community were obtained during June and July, 1934, and for the beech-maple community in July and August, 1937. Heath balds and alder balds were surveyed during July and August, 1934, and grassy balds in July and August, 1936.

The nomenclature follows Sudworth (1927) for trees, Gray's New Manual of Botany (7th edition) for shrubs and herbs except a few found in Small (1933), and Blomquist (1934) for pteridophytes.

A complete collection representing species involved in this study has been deposited in the Herbarium of Duke University, Durham, North Carolina.

COLLECTION OF SUCCESSIONAL DATA

During the three summers spent on Roan Mountain, observations were made in order to discover successional trends. In 1937 a concentrated attempt was made to discover evidence tending toward an explanation of this problem. Notes were made in the field as a result of such observation and thinking, and numerous photographs along ecotones were made for future study. In addition, certain statistical methods were employed, including *belt transects*, *strip samples*, and *chart quadrats*. Areas thus investigated were permanently marked for future study.

BELT TRANSECTS

Three belt transects were established across the ecotone between the grassy bald community and the spruce-fir community. Only individuals of woody species and moss mats were mapped, other species

being listed by coverage classes for each square meter of the 1-meter strip and for each 4 square meters of the 2-meter strip. The two 1-meter belt transects were on Cloudland, 6,100 feet altitude, and the 2-meter transect was at Carvers Gap, 5,500 feet altitude.

STRIP SAMPLES

A set of strip samples was used on Round Bald, largest grassy bald area of the mountain. This set consisted of 355 contiguous 2 by 2 meter quadrats along a north-south line which extends across the crest of the bald and into the beech-maple on either side. Two similar sets of samples were employed on Roan High Knob to determine the relative importance of alder, heath, and conifers. The first set consisted of 37 quadrats 2 by 2 meters spaced along a line extending from the highest point of the mountain to the edge of the spruce-fir forest to the north.² The other set consisted of 25 quadrats of the same size and spacing along a line extending from the same point on the knob to a point southward within the grassy bald.

CHART QUADRATS

Two permanent chart quadrats, 2 by 2 meters each, were established on mineral soil at 6,100 and 6,200 feet altitude, respectively, in order to study establishment of herbs, shrubs, and conifers. Another permanent chart quadrat, 4 by 4 meters, was established in the grassy bald immediately west of Carvers Gap to study invasion of woody species, especially conifers.

A number of other miscellaneous samples were taken across transition lines and in cut-over spruce-fir, but space does not allow their treatment.

VEGETATION

Following Schimper (1903), the vegetation would be divided into forest and grassland, but since certain shrubs are dominant in the grassland area as "thicket communities," it seems preferable to refer to treeless areas as balds.³ Three forest communities are present on Roan Mountain and they are zoned altitudinally as follows: (1) oak-chestnut community, generally below an altitude of 3,500 feet but extending up some of the ridges to 4,000 feet; (2) beech-maple community between 3,500 and 5,000 feet, by far the most extensive of the area; and (3) spruce-fir community, above 5,000 feet. Most of the original area of the oak-chestnut community has been cleared for cultivation. Practically all trees of any size have been removed for lumber. Most of the chestnut was killed or seriously injured by blight before it was cut. This community is now too poorly represented to justify its analysis or further description.

The balds occur on long, broad ridges above 5,500 feet altitude and, according to most estimates, cover

² The beginning point was a marker of the United States Geological Survey embedded in a huge boulder on the summit.

³ Early settlers doubtless named these areas "balds" since each is surrounded by forest vegetation and, at a distance, appears like a bald spot on a man's head.

an area of more than 1,000 acres, mostly with a southern exposure. Three major communities are located approximately as follows: (1) rhododendron balds, above 6,000 feet altitude and west of Carvers Gap; (2) alder balds, in moister areas of southern slopes east of Carvers Gap; and (3) grassy balds, occurring throughout the full extent of the bald area but with best development in the vicinity of Carvers Gap.

BEECH-MAPLE COMMUNITY

Three stands were located in which no fires have been known or cuttings made except half a century ago. Stands A and B are each approximately 5 acres, Stand C, 6.25 acres.

Location of Stands.

Stand A is located on the north slope at an altitude of approximately 4,600 feet, and nearly a mile northeast of Round Bald (Fig. 1). It is approximately 50 yards from a small stream on the east and extends westward over the crest of a gently sloping ridge. The soil surface is rolling with an average slope of about 14 degrees toward the northeast. Stand B is on the south slope, one-half mile south of Carvers Gap at 4,800 feet altitude. It extends over a broad ridge and faces south with an average slope of about 10 degrees. Stand C is located at the same altitude one mile eastward, and faces south with a slope of approximately 8 degrees. In all stands soil is relatively free from surface rocks and outcrops. Stand C is located on what might be termed a "shelf." Soil is more productive in this stand due, perhaps, to its greater depth.

Stratification.

In the beech-maple community, four layers can be recognized: (1) *tree layer*, usually consisting of superior and inferior layers; (2) *shrub layer*, consisting of shrubs and tree saplings (designated by Cain (1932) as "transgressives"); (3) *herb layer*, composed of herbs and seedlings of trees and shrubs; and (4) *moss or ground layer*, consisting principally of mosses and lichens. The approximate average vertical location of each of these layers and its coverage class is shown graphically in Figure 5. On the whole, there is no clear-cut separation of layers but rather much overlapping. This is especially true of individuals of tree species which dominate the shrub layer as well as both tree layers.

TREE LAYER

The superior tree layer ranges from 40 to 60 feet in height and from 60 to 90 percent coverage, with an average height of 50 feet and an average coverage of about 70 percent (Figs. 5 and 7). The inferior layer ranges from 10 to 30 feet in height but with more foliage between 20 to 30 feet. In general, the canopy is quite irregular, since it represents an uneven-aged mixed stand of trees. A few of the larger trees, occasionally reaching a height of 70 feet, stand above the superior layer as "dominants," according to the crown classification of foresters.

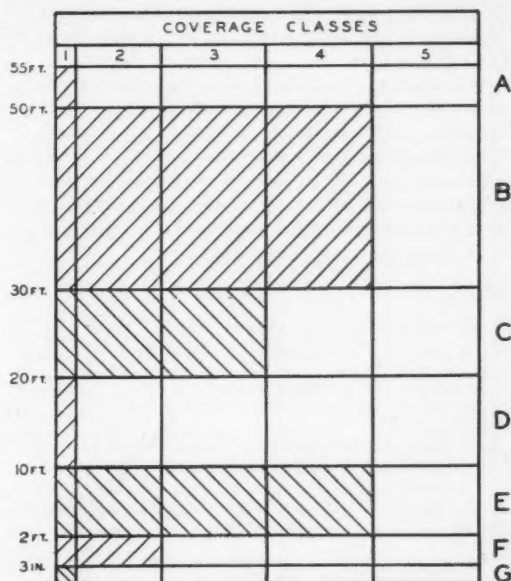


FIG. 5. A combination of coverage class data and stratification for the beech-maple community. (Based on coverage data and recorded from the quadrats and stratification diagrams made in the field at each tree quadrat.)

A. Trees of superior layer overtopping forest canopy. Mostly *Acer saccharum*.

B. Superior tree layer of *Fagus grandifolia*, *Acer saccharum*, and *Betula lutea*.

C. Upper inferior tree layer of *Fagus grandifolia* and *Acer saccharum*.

D. Lower inferior tree layer of *Fagus grandifolia*, *Acer saccharum*, *A. spicatum*, and *A. pennsylvanicum*.

E. Shrub layer of *Fagus grandifolia*, *Acer saccharum*, *Viburnum alnifolium*, and *Rubus canadensis*.

F. Herb layer dominated by *Dryopteris*, *Eupatorium*, and *Impatiens*.

G. Moss layer consisting of various mosses and lichens.

Frequency.

In Table 2 is presented a complete list of species occurring in the beech-maple community, as determined by quadrat data. The frequency index (frequency percentage) for each species is shown for separate stands as well as for the community as a whole.

Fagus grandifolia, with a frequency of 95 percent for the stand on north slope and 100 percent for each stand on south slope, is most frequent tree species. The one quadrat of the north slope in which this species did not occur was in an outwash which was very moist and was dominated by *Betula nigra* and *Betula lenta*. *Acer saccharum* ranks second, with a frequency of 75 percent for north slope, 55 percent and 95 percent, respectively, for south slope stands, and with an average of 75 percent for the community. *Aesculus octandra* and *Betula lutea* each show the same frequency for the community, 11.7 percent, with slight differences as to stands. Each of the remaining 9 species has a frequency below 10 percent, and it may be noted that *Acer pennsylvanicum* occurs

in all three stands, that *Amelanchier laevis* occurs in two stands, and each of the other 7 species occurs in but one stand.

The important trees of this community are *Fagus grandifolia*, *Acer saccharum*, *Betula lutea*, *Aesculus octandra*, and *Amelanchier laevis* as superior or "overstory" species, and *Acer spicatum* and *Acer pennsylvanicum* as inferior or "understory" species. *Picea rubra* is an accidental intruder from the spruce-fir forest above, and *Crataegus* sp. is a rare intruder from the higher ridges and balds.

Density.

Densities of woody species above 1 foot high by stands and for the community as a whole are shown

TABLE 2. Frequency and coverage data for species occurring in the beech-maple community. (July and August, 1937.)

Floristic list	Frequency percent				Distribution of coverage classes for the community					
Stand:	A	B	C	Community						
Altitude:	4,600	4,800	4,800							
Exposure:	NE	S	S							
Slope:	14°	10°	8°		0	1	2	3	4	5
Trees¹										
<i>Acer pennsylvanicum</i>	5	10	5	6.7						
<i>Acer saccharum</i>	75	55	95	75.0						
<i>Acer spicatum</i>	15			5.0						
<i>Aesculus octandra</i>	10	15	10	11.7						
<i>Amelanchier laevis</i>	10	15		8.3						
<i>Betula lenta</i>	10			3.3						
<i>Betula nigra</i>	5			1.7						
<i>Betula lutea</i>	15	5	15	11.7						
<i>Crataegus</i> sp.			5	1.7						
<i>Fagus grandifolia</i>	95	100	100	98.2						
<i>Picea rubra</i>		5		1.7						
<i>Prunus serotina</i>		5		1.7						
Shrubs²										
<i>Cornus alternifolia</i>	5			1.7						
<i>Ribes rotundifolium</i>	15			5.0						
<i>Rubus canadensis</i>	10	10		6.7						
<i>Sambucus canadensis</i>	5			1.7						
<i>Viburnum alnifolium</i>	30	10		13.3						
Pteridophytes³										
<i>Athyrium thelypteroides</i>	1			.3						
<i>Dryopteris dilatata</i>	46	2	1	17.0	11	25	14	1		
<i>Polypodium virginianum</i>	3			1.0	1	1				
<i>Polystichum acrostichoides</i>	10			3.3	1	6	3			
<i>Lycopodium lucidulum</i>	27	1		9.3	10	13	3	2		
Herbs³										
<i>Actaea alba</i>	5		4	4.0	3	5	4			
<i>Allium tricoccum</i>	7			2.3	3	3				
<i>Arisaema triphyllum</i>	20	36	47	31.0	77	19				
<i>Aster divaricatus</i>	54	29	16	33.0	67	30	2			
<i>Aster acuminatus</i>	10			3.3	5	4	1			
<i>Carex leptalea</i>	1			.3	1					
<i>Carex lucorum</i>	16	62	5	27.7	15	21	23	18	6	
<i>Chelone Lyoni</i>	7			2.3	3	3	1			
<i>Clematis Viorna</i>	1			.3	1					
<i>Clintonia umbellulata</i>	5			1.7	2	3				
<i>Cimicifuga racemosa</i>	12			4.0	5	4	3			
<i>Circaea alpina</i>	2			.7	1		1			
<i>Danthonia compressa</i>	1			.3	1					
<i>Diocoreia villosa</i> var. <i>glabra</i>		7	2	3.0	7	2				
<i>Diphylleia cymosa</i>	2			.7	2					
<i>Eupatorium roanensis</i>	22	34	32	27.0	37	34	5	5	1	

TABLE 2 (Continued)

Floristic list	Frequency percent				Distribution of coverage classes for the community					
Stand:	A	B	C	Community						
Altitude:	4,600	4,800	4,800							
Exposure:	NE	S	S							
Slope:	14°	10°	8°		0	1	2	3	4	5
<i>Galium triflorum</i>	6	1	1	2.7	4	4				
<i>Heuchera villosa</i>	4			1.3	4					
<i>Impatiens biflora</i>	40	2	5	15.0	19	20	4	3	1	
<i>Empatiens pallida</i>	4		3	2.3	5	2				
<i>Isopyrum biternatum</i>	1			.3	1					
<i>Maianthemum canadense</i>	13	3		5.3	8	8				
<i>Melanthium parviflorum</i>	11	9	1	7.0	120					
<i>Mitella diphylla</i>	2			.7	1	1				
<i>Monotropa uniflora</i>	2			.7	1	1				
<i>Nabalus cylindricus</i>			2	.7	2	2				
<i>Oxalis acetosella</i>	3			.7	2	2				
<i>Podophyllum peltatum</i>			2	.7	2	2				
<i>Prenanthes altissima</i>	2			.7	1	1				
<i>Saxifraga leucanthemifolia</i>	2			.7	1	1				
<i>Sedum ternatum</i>	1			.3	1	1				
<i>Smilacina racemosa</i>	4	4	4	4.0	11	1				
<i>Solidago squarrosa</i>	1	4	6	3.7	8	2	1			
<i>Stellaria pubera</i>	50	8	5	21.0	30	28	5			
<i>Streptopus roseus</i>	5			1.7	3	2				
<i>Troutvetteria carolinensis</i>	2		7	3.0	9					
<i>Urtica dioica</i>	12	2	5	6.3	10	5	3	1		
<i>Veronica officinalis</i>	1			.3	1					
<i>Viola cucullata</i>	9			3.0	7	5	1			
<i>Viola canadensis</i>	2			.7	2					
Moss and lichen cover	32	11	10	17.6	11	17	20	3	1	1

¹Based on 60 quadrats 10 by 10 meters, 20 in each stand.

²Based on 60 quadrats 4 by 4 meters, 20 in each stand.

³All herbaceous data based on 300 quadrats 1 by 1 meter, 100 in each stand.

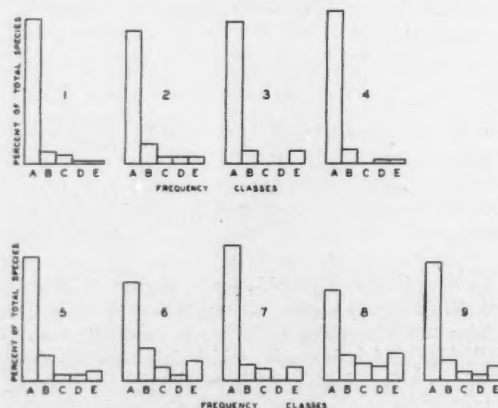


FIG. 6. Frequency class diagrams of the forest communities.

1. Stand A, beech-maple community.
2. Stand B, beech-maple.
3. Stand C, beech-maple.
4. The beech-maple community as a whole.
5. Stand A, spruce-fir community.
6. Stand B, spruce-fir.
7. The spruce-fir community as a whole.
8. Raunkiaer's "normal."
9. Kenoyer's "normal."

in Table 3. Of the total individuals of tree species, 73 percent belong to *Fagus grandifolia*, 22 percent to *Acer saccharum*, 2.7 percent to *Acer spicatum*, 1 per-



FIG. 7. Beech-maple forest of the north slope as viewed from Roan High Bluff, altitude 6,267 feet. Note presence of spruce and fir at the higher altitudes. The cleared fields below are at an altitude of about 3,500 feet.

cent to *Acer pennsylvanicum*, and 1.3 percent to the other 9 species. The north slope supports higher densities than the south slope. This is especially noticeable for *Acer spicatum* and *Acer pennsylvanicum*, 99 percent of which occur on the north slope.

Densities of tree species by five size classes are shown in Table 4. Only two species, *Fagus grandifolia* and *Acer saccharum*, occur in all classes. This indicates that these species are maintaining themselves. The mortality of *Acer saccharum* in the early stages is high as compared to *Fagus grandifolia*, since more than 95 percent of seedlings die before reaching a height of 1 foot. The 67 individuals under 1 foot high recorded for *Fagus grandifolia* represent seedlings and this number does not include the numerous root suckers. *Acer spicatum* and *Acer pennsylvanicum* are not important trees, since they do not reach a d.b.h. of more than 3 inches. About 90 percent of the former and 66 percent of the latter die before they reach a height of 1 foot. *Prunus serotina*, *Fraxinus* sp., and *Quercus velutina* are less than 1 inch



FIG. 8. Winter aspect of beech-maple forest community showing something of density and size classes. North slope at 4,800 feet altitude. Photographed January, 1936.

TABLE 3. Number per acre of woody individuals 1 foot high and over occurring in different stands of the beech-maple community.¹ Stand A is on north slope and stands B and C are on south slope.

Species	Individuals per acre			
	Stand A	Stand B	Stand C	Community
Trees				
<i>Fagus grandifolia</i>	4,688	4,972	3,040	4,233
<i>Acer saccharum</i>	1,906	562	1,316	1,262
<i>Acer spicatum</i>	474	158
<i>Acer pennsylvanicum</i>	194	4	2	67
<i>Aesculus ocutandra</i>	6	80	16	34
<i>Betula lutea</i>	22	28	10	20
<i>Betula nigra</i>	30	10
<i>Prunus serotina</i>	14	5
<i>Fraxinus</i> sp.	12	4
<i>Tilia</i> sp.	12	4
<i>Amelanchier laevis</i>	4	6	3
<i>Betula lenta</i>	6	2
<i>Picea rubra</i>	2	1
Total trees	7,342	5,680	4,382	5,802
Shrubs				
<i>Viburnum alniifolium</i>	762	50	272
<i>Rubus canadensis</i>	488	88	192
<i>Ribes rotundifolium</i>	88	29
<i>Sambucus racemosa</i>	12	4
Total shrubs	1,350	138	496
Total trees and shrubs	8,692	5,818	4,382	6,298

¹The basic figures for individuals 1 inch d.b.h. or larger were obtained from 20 quadrats 10 by 10 meters for each stand; the basic figures for those under 1 inch d.b.h. were obtained from 20 quadrats 4 by 4 meters for each stand and multiplied by proper factor to make them equivalent to as many 10 by 10 meter quadrats. These values were then combined and their sums multiplied by 2 to change to an acre basis.

TABLE 4. Density per acre of tree species by five size classes as represented in the beech-maple community.¹ (Based on 60 quadrats 10 by 10 meters.)

Species	Up to 1 ft. high	1 ft. to 1 in. d.b.h.	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. and over	Total
<i>Acer saccharum</i>	18,952	1,096	132	25	8	20,213
<i>Fagus grandifolia</i>	67	3,758	272	147	56	4,300
<i>Acer spicatum</i>	1,387	146	11	1	1,545
<i>Betula lutea</i>	293	13	1	6	313
<i>Prunus serotina</i>	320	4	1	325
<i>Acer pennsylvanicum</i>	186	63	4	253
<i>Betula lenta</i>	80	2	82
<i>Fraxinus americana</i>	67	4	71
<i>Aesculus octandra</i>	25	5	3	1	34
<i>Quercus velutina</i>	27	27
<i>Betula nigra</i>	8	1	1	10
<i>Amelanchier laevis</i>	1	3	4
<i>Picea rubra</i>	1	1
Total.....	21,379	5,100	434	181	75	27,169

	Number	Percent	
Number and percentage of species occurring in.....	five classes....	2	14.3
	four classes....	2	14.3
	three classes....	4	28.6
	two classes....	3	21.4
	one class.....	3	21.4
Total.....	14	100.0	

¹Basic figures for sizes under 1 inch d.b.h. were taken from the 4 by 4 meter quadrants and multiplied by the figure necessary to make total density equivalent to 1 acre. Basic figures for sizes above 1 inch d.b.h. were reduced to an acre basis.

d.b.h. except one *Prunus* which was 10 inches d.b.h. These occurred on the south slope and indications are that they would never be expected to play an important role in tree layer. *Quercus*, present in the quadrats only as seedlings, is a tree rarely found on Roan Mountain, although a few large specimens were observed on ridges of south slopes between 4,500 and 5,000 feet altitude.

Basal Area.

Basal area data for trees of the beech-maple community are shown in Table 5. Basal area per acre for all trees by stands varies from 127.64 square feet in Stand A to 174.82 square feet in Stand C. But since

TABLE 5. Basal area and density per acre of trees of the beech-maple community. The upper figure of each pair represents basal area and the lower one, density. (Based on 20 quadrats, 10 by 10 meters, in each stand.)

Stands:	Basal area in square feet				Percent of total basal area	Average basal area per stem (sq. ft.)
	A	B	C	Community		
<i>Fagus grandifolia</i> . . .	87.10 400.00	106.94 596.00	108.38 428.00	100.81 474.67	65.99	.212
<i>Acer saccharum</i> . . .	14.82 106.00	34.02 50.00	27.10 340.00	25.31 765.34	16.67	.152
<i>Betula lutea</i> . . .	15.64 10.00	1.84 2.00	33.30 10.00	16.93 7.33	11.16	2.309
<i>Amelanchier laevis</i> . . .	2.20 4.00	6.14 6.00	2.78 3.33	1.83	.834
<i>Aesculus octandra</i>12 6.00	3.00 18.00	4.38 4.00	2.50 9.33	1.58	.257
<i>Betula nigra</i> . . .	4.08 30.00	1.36 10.00	.88	.136
<i>Acer spicatum</i> . . .	2.00 38.0067 12.67	.44	.053
<i>Crataegus</i> sp.	1.64 4.00	.55 1.33	.36	.410
<i>Betula lenta</i> . . .	1.60 6.0053 2.00	.35	.267
<i>Prunus serotina</i>	1.30 2.0043 .67	.28	.650
<i>Acer pennsylvanicum</i>08 6.00	.26 4.00	.02 2.00	.12 4.00	.08	.030
<i>Picea rubra</i>02 2.0001 .67010
Totals: (Basal area: . . .)	127.64	153.54	174.82	152.00	100.00	
(Density: . . .)	606.00	680.00	788.00	691.30		

the density increases in about the same ratio as basal area the sizes of trees average about the same for all stands. The relative importance of each species in the community is best shown by the percentage each represents of total basal area of all species present. *Fagus grandifolia* ranks first with 65.99 percent, followed in order by *Acer saccharum* with 16.67 percent, *Betula lutea* with 11.16 percent, *Amelanchier laevis* with 1.83 percent, *Aesculus octandra* with 1.58 percent, and the remaining 8 species with less than 1 percent each. Average basal area per stem for each of the three important trees is: *Fagus grandifolia*, 0.212 square feet; *Acer saccharum*, 0.152 square feet; and *Betula lutea*, 2.309 square feet. This means that the stems of *Betula lutea* average much larger than any other species.

TABLE 6. A comparison of basal area per acre of trees 1 inch and above, of the beech-maple community by three size classes. (Based on 60 quadrats 10 by 10 meters.)

Species	Basal area per acre			
	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. and over	Total
<i>Fagus grandifolia</i> . . .	7.15	39.71	53.95	100.81
<i>Acer saccharum</i> . . .	3.51	4.15	17.65	25.31
<i>Betula lutea</i>02	.18	16.73	16.93
<i>Amelanchier laevis</i>29	2.49	2.78
<i>Aesculus octandra</i>13	.43	1.84	2.40
<i>Betula nigra</i>25	.29	.82	1.36
<i>Acer spicatum</i>41	.2566
<i>Crataegus</i> sp.11	.44	.55
<i>Betula lenta</i>5353
<i>Prunus serotina</i>44	.44
<i>Acer pennsylvanicum</i>1212
<i>Picea rubra</i>0101
Totals . . .	11.81	45.94	94.36	151.91

¹Basic figures from 60 quadrats 10 by 10 meters were multiplied by 2/3 to reduce them to an acre basis.

A comparison of basal area by size classes is shown in Table 6. *Acer saccharum* has a higher percentage of its total basal area in the 1- to 3-inch class than does *Fagus grandifolia*, which may indicate a future trend toward more *Acer saccharum*. On the other hand, *Betula lutea* shows essentially all of its basal area in the 10-inch class and above, indicating its deterioration in the community. But the mortality of *Betula lutea* is lowest of any species within the community due to its unusual ability to withstand wind-fall and heart rot.

Phytographs.

Five of the more important species of trees are presented graphically in Figure 9 by means of phytographs (Lutz, 1930). Four axes of phytographs

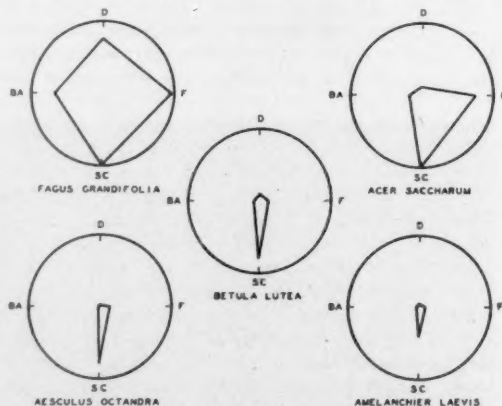


FIG. 9. Phytographs of the more important tree species of the beech-maple community. Constructed from data shown in Table 7.

Legend:

D, percentage of total density, 10 inches d.b.h. and over.
F, frequency percentage, 1 inch d.b.h. and over.
SC, representation in the different size classes.
BA, percentage of total basal area.

herein employed are percentage expressions of (1) abundance of stems 10 inches d.b.h. or over, (2) frequency of stems 1 inch d.b.h. or over, (3) number of size classes in which the species is found, and (4) basal area. Data for construction of the phytographs are shown in Table 7.

TABLE 7. Data for construction of phytographs: 5 species. (Based on data from tables—Values on percentage of total basis.)

Species	Radius 1; Abundance above 10 in. d.b.h.	Radius 2; Frequency above 1 in. d.b.h.	Radius 3; Number of size classes	Radius 4; basal area
<i>Fagus grandifolia</i> . . .	74.7	98.2	100	66.4
<i>Acer saccharum</i>	10.7	75.0	100	16.7
<i>Betula lutea</i>	8.0	11.7	80	11.2
<i>Aesculus octandra</i> . . .	1.3	11.7	80	1.6
<i>Amelanchier laevis</i> . . .	4.0	8.3	40	1.8

Fagus grandifolia is the most important tree of the community, the first dominant, and is followed by *Acer saccharum* as codominant. The more important associates are *Betula lutea*, *Aesculus octandra*, and *Amelanchier laevis*.

SHRUB LAYER

Frequency.

Only 6 species of shrubs were recorded in the beech-maple community, with 5 appearing in Stand A, 3 in Stand B and none in Stand C (Table 2). *Viburnum alnifolium*, frequency 11.7 percent, ranks first, with *Rubus canadensis*, frequency 6.7 percent, occurring in open places, and *Ribes rotundifolium*, frequency 5 percent, in moist sites. Each of the other three species, *Cornus alternifolia*, *Sambucus canadensis*, and *Sambucus racemosa*, has a frequency of 1.7 percent.

Density.

Viburnum alnifolium shows the greatest density of any shrub, with 94 percent of the total count appearing on the north slope in Stand A, 6 percent on the south slope in Stand B, and none in Stand C. *Rubus canadensis* ranks second with 85 percent of the plants being on the north slope and 15 percent on the south slope in Stand B. The total density of all shrubs 1 foot high or more is 744 as compared to 5,109 tree stems 1 foot high to 1 inch d.b.h. Basic figures for the above percentages are presented in Table 2.

Densities of woody species of the shrub layer by height classes are shown in Table 8. Shrub species represent only 9 percent of total density of all species 1 to 12 feet high (shrub layer). Thus it is seen that the shrub layer is dominated by transgressives. Of these, 85 percent are *Fagus grandifolia* and *Acer saccharum* and at least three fourths of the total individuals are *Fagus grandifolia*.

HERB LAYER

Pteridophytes and herbs (including grasses and sedges) are included in the herb layer. Seedlings of both trees and shrubs are temporarily present in this

TABLE 8. Density per acre of the woody species, up to 12 feet high, by three height classes as represented in the beech-maple community. (Based on 60 quadrats, 4 by 4 meters, 0.24 acre.)¹

Species	Up to 1 ft.	1 ft.-3 ft.	3 ft.-12 ft.	Total
Trees				
<i>Acer saccharum</i>	18,950	479	617	20,046
<i>Fagus grandifolia</i>	67	2,333	1,425	3,825
<i>Acer spicatum</i>	1,388	121	25	1,534
<i>Prunus serotina</i>	321	4	325
<i>Betula lutea</i>	292	13	305
<i>Acer pennsylvanicum</i> . . .	188	58	4	250
<i>Crataegus</i> sp.	92	92
<i>Betula lenta</i>	79	79
<i>Fraxinus</i> sp.	67	4	71
<i>Aesculus octandra</i>	21	4	25
<i>Tilia</i> sp.	4	4
Shrubs				
<i>Viburnum alnifolium</i> . . .	79	208	63	350
<i>Rubus canadensis</i>	67	154	38	259
<i>Ribes rotundifolium</i> . . .	92	29	121
<i>Sambucus canadensis</i>	4	4
<i>Sambucus racemosa</i>	4	4
<i>Cornus alternifolia</i>	4	4
Total	21,682	3,440	2,176	27,298

¹Basic figures for reproduction under 6 inches were taken from 300 quadrats 1 by 1 meter and changed to an acre basis. Trees 1 inch d.b.h. and over were not included.

layer but are not considered at this point since they belong to superior layers when mature.

Frequency.

The only fern of importance is *Dryopteris dilatata*, which is confined almost exclusively to the north slope and has a frequency of 17 percent for the community. The other three species encountered, namely, *Polystichum acrostichoides*, *Polypodium virginianum*, and *Asplenium acrostichoides* are confined exclusively to the north slope where they show frequencies of 10 percent, 3 percent, and 1 percent, respectively, for the stands. *Lycopodium lucidulum* is confined essentially to the north slope where it shows a frequency of 27 percent as compared to 0.5 percent for the south slope.

Of the 40 species of herbs, only 11 species occur in all these stands, and 6 of these show a frequency above 10 percent for the community. These are: *Aster divaricatus*, 33 percent, *Arisaema triphyllum*, 31 percent, *Carex lucorum*, 27.7 percent, *Eupatorium roanensis*, 27 percent, *Stellaria pubera*, 21 percent, and *Impatiens biflora*, 15 percent. The others are: *Galium triflorum*, 2.7 percent, *Melanthium parviflorum*, 7 percent; *Smilacina racemosa*, 4 percent, *Solidago squarrosa*, 3.7 percent, and *Urtica dioica*, 6.3 percent. These 11 species are reasonably well distributed in all three stands of the community, with the exception of *Carex lucorum*, which occurs with a frequency of 5 percent and 62 percent, respectively, for stands of the southern slope, as compared to 16 percent for the stand on northern slope. *Impatiens biflora* and *Stellaria pubera* are 6 to 8 times more frequent on the north slope than on the south slope. Forty-two of the 45 species of the herb layer occur on north slope, while only 20 species are found on

south slope with 15 species in Stand B and 18 species in Stand C. The most characteristic species of the herb layer are: *Actaea alba*, *Lycopodium lucidulum*, *Cimicifuga racemosa*, *Eupatorium roanensis*, *Maianthemum canadense*, *Smilacina racemosa*, *Urtica dioica*, *Arisaema triphyllum*, *Melanthium parviflorum*, *Impatiens biflora*, *Carex lucorum*, and *Stellaria pubera*.

Coverage.

Coverage classes for all species present in the herb layer are shown in Table 2. *Carex lucorum*, with an average coverage of class 2 for the community, is highest for any species in the herb layer and its highest coverage is in Stand B of south slope. This species covers approximately 15 percent of total quadrat area although a variation of from 1 to 75 percent occurs among individual quadrats. It is most abundant where canopy is relatively open, as along the broad ridges of upper slopes. Only three species show a coverage of class 1, namely, *Dryopteris dilatata*, *Eupatorium roanensis*, and *Impatiens biflora*. The other 41 species of the community are present with a coverage less than 1 percent; however, a few of them, as *Cimicifuga racemosa* and *Urtica dioica*, show a coverage of class 1 in Stand A. Total coverage of all herbs is only class 2 for the community, which means that less than 25 percent of total ground surface is shaded by plants of herb layer.

Woody seedlings.

Quadrat data show 19,452 seedlings (under 1 foot high) per acre for the community. Of these, 18,027 belong to *Acer saccharum* which shows a frequency of 90 percent, while only 67 belong to *Fagus grandifolia* which shows a frequency of 1.3 percent. But it must be remembered that *Acer* reproduces mostly seedlings while *Fagus* commonly reproduces by root suckers. *Prunus serotina*, *Betula lutea*, and *Acer pennsylvanicum* show a combined total of 786 individuals per acre and are the only other woody species with more than 100 seedlings each per acre. The shrubs, *Ribes rotundifolium* and *Viburnum alnifolium* show 93 individuals each per acre. The north slope supports practically all the shrub seedlings recorded for the community, indicating that the north slope is more mesic than the south slope.

MOSS LAYER

No attempt was made to consider the different species of mosses and lichens, but they were recorded as a layer and coverage indicated if the layer was present. In general, when moss occurred lichens were present also. Frequencies for this layer were as follows: Stand A, 32 percent; Stand B, 11 percent; and Stand C, 10 percent. The average for the community was 17.6 percent. Coverage for the community was class 1, and was much higher on the north slope than on the south slope.

BEECH-MAPLE COMMUNITY AS A WHOLE

The following four layers were recognized: tree layer, shrub layer, herb layer, and ground layer. The tree layer consists of 12 species and is dominated by



FIG. 10. Interior view of beech-maple forest as it occurs in Stand A of the north slope. Note uneven age condition of trees. *Dryopteris*, *Smilacina*, *Cimicifuga*, and *Allium* may be seen in the herb layer.

beech and maple but yellow birch becomes more important with increased altitude until it forms "consociations" at upper limits of this hardwood zone. The shrub layer consists of 6 species only and these represent only 9 percent of woody individuals from 1 to 12 feet high. The remaining 91 percent is represented by tree transgressives which dominate the shrub layer. Hobble bush (*Viburnum alnifolium*) is most important shrub present. Of 41 species present in the herb layer, only four (*Carex lucorum*, *Dryopteris dilatata*, *Eupatorium roanensis*, and *Impatiens biflora*) cover as much as class 1 (1 to 5 percent of the surface). One species, *Carex lucorum*, covers class 2 (5 to 25 percent of the surface). A light ground cover of mosses and lichens covered less than 5 percent of the surface.

As indicated by basal area data, this forest community shows a better development of trees on southern slopes than on northern slopes of Roan Mountain. Frequency and coverage data show a better development of shrubs, herbs, and mosses on northern slopes, except for *Carex lucorum*, which shows its best development on southern slopes. As evidenced by the vigorous distribution of trees of all sizes and ages, it appears that the dominants of this community are being maintained.

SPRUCE-FIR COMMUNITY

Location of Stands.

Fortunately a virgin area was located and two stands studied before cutting began.⁴ Stand A was sampled by laying out 20 tree and 20 shrub quadrats distributed at 50-meter intervals according to the Latin square method and by 100 herb quadrats located at 10-meter intervals along control lines. Stand B was sampled by laying out 12 tree and 12 shrub quadrats accompanied by 60 herb quadrats distributed at 10-meter intervals along control lines. Stand A was located about one-half mile north of the United

⁴ This community was studied early in the summer of 1934. By the time quadrat work was completed, more than half the area had been cut. Trees were cut from a few quadrat areas in less than an hour after they had been studied.

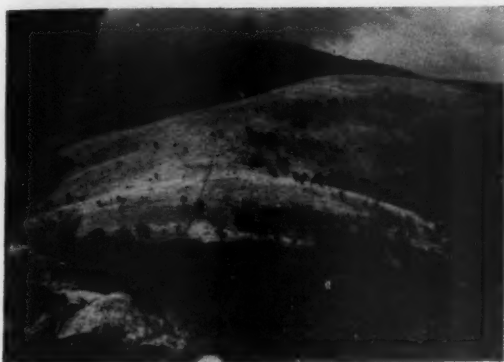


FIG. 11. Upper limit of hardwood forest as seen from Jane Bald, 6,000 feet altitude, looking west toward Roan High Knob (distant center). Note sharp margin of *Fagus* bordering grassy bald on the south slope (left) and orchard condition of *Aesculus* on the north slope (right). *Alnus* thicket appears in the foreground.

States Geological Survey marker on Roan High Bluff (6,267 feet altitude) at an altitude of 5,400 feet. Stand B was located about half way between Stand A and the geological marker at 5,800 feet altitude. Topography of the area immediately north and west of Roan High Bluff in which these stands were located is the most rugged part of the mountain. The slope ranges from 10 degrees to vertical cliffs 10 to

50 feet high. Topography is also quite irregular, with slopes facing all points of compass except south, but the main exposure is northwest. Soil is moist and fertile and usually shallow, except in small depressions and "shelves" at heads of coves. About 10 percent of area is exposed rock, mostly outcrop, which is usually covered with mosses, lichens, and ferns.

Windfall seems to have been a most important single natural factor affecting vegetation, and has been more severe on heavily exposed ridges. In one small area, 13 trees above 10 inches d.b.h. were counted which had been blown down at different times. Near the summit on the north slope, a landslide had occurred which left about 200 square meters of exposed rock. A few fir trees on the higher spurs had been killed by lightning. So far as could be learned no disturbance had been caused by man or his domestic animals within the area sampled.

Stratification.

In this community four major layers occur which are better differentiated than those of the beech-

TABLE 9. Frequency and coverage data for species occurring in the spruce-fir community. (June and July, 1934.)

Floristic list	Frequency percent			Distribution of coverage classes for the community					
	A	B	Community						
Stand:	5,400	5,800							
Altitude:	NW	NW	NW						
Exposure:	20°	30°							
Slope:				0	1	2	3	4	5
Trees¹									
<i>Abies Fraseri</i>	95	100	97.5						
<i>Acer spicatum</i>	25	75	50						
<i>Aesculus octandra</i>	5	8.3	6.7						
<i>Betula picea</i>	80	91.7	85.8						
<i>Fagus grandifolia</i>	10		5						
<i>Picea rubra</i>	100	100	100.						
<i>Prunus pennsylvanica</i>	5		2.5						
<i>Sorbus americana</i>	15	25	20						
Shrubs²									
<i>Cornus alternifolia</i>	20	8.3	14.2						
<i>Hydrangea arborescens</i>	5		2.5						
<i>Lonicera canadensis</i>	5		2.5						
<i>Rhododendron catawbiense</i>	20	50	35						
<i>Ribes rotundifolium</i>	5	8.3	6.7						
<i>Rubus canadensis</i>		16.7	8.4						
<i>Sambucus racemosa</i>	5		2.5						
<i>Vaccinium erythrocarpum</i>	35	56.7	45.9						
<i>Viburnum alnifolium</i>	50	25	37.5						
Pteridophytes³									
<i>Dryopteris dilatata</i>	80	88.3	84.1	35	18	17	2	4	
<i>Athyrium asplenoides</i>		30	15		6	8	3	1	
<i>Polystichum acrostichoides</i>	2		1		2				
<i>Polypodium virginianum</i>	25	16.6	20.8		2	17	9	5	
<i>Lycopodium lucidulum</i>	33	30	31.5		2	40	7	2	
Herbs³									
<i>Agrostis hyemalis</i>		3.3	1.7	2					
<i>Agrostis perennans</i>	6		3		6				
<i>Angelica Curtisii</i>	1		0.5			1			
<i>Arisaema triphyllum</i>	15	1.6	8.3		1	11	2	2	
<i>Aster acuminatus</i>	19	15	17		20	3	3	1	
<i>Aster divaricatus</i>	32	40	36		7	27	17	4	1
<i>Cardamine Clematitis</i>	5	3.3	4.2		2	4			1
<i>Carex gracillima</i>	10	11.6	5.8		10	1			

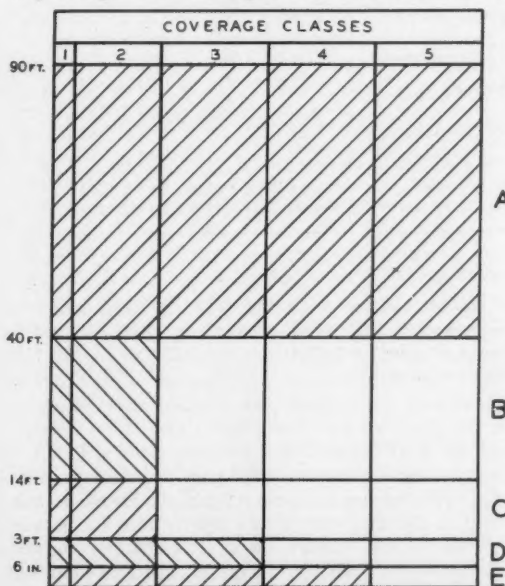


FIG. 12. Stratification-coverage diagram for Stand A of the spruce-fir community.

- A. Superior tree layer of *Picea* and *Abies*.
- B. Inferior tree layer of *Betula* with *Picea* and *Abies*.
- C. Shrub layer of *Rhododendron*, *Vaccinium*, and *Viburnum*.
- D. Herb layer dominated by *Dryopteris*.
- E. Moss or ground layer of mosses interwoven with *Oxalis*.

TABLE 9 (Continued)

Floristic list	Frequency percent			Distribution of coverage classes for the community					
	A	B	Community	0	1	2	3	4	5
Stand:.....	5,400	5,800						
Altitude:.....	NW	NW	NW						
Exposure:.....	20°	30°						
Slope:.....									
<i>Carex trisperma</i>	1.6	0.8	1						
<i>Carex leptalea</i>	1	11.6	6.3	3	5				
<i>Chelone Lyoni</i>	18	20	19	3	19	8			
<i>Cimicifuga racemosa</i>	5	2.5	3	2					
<i>Circaea alpina</i>	25	10	17.5	4	24	2	1		
<i>Clintonia borealis</i>	9	23.3	16.2	4	13	5	1		
<i>Eupatorium roanensis</i>	1.6	0.8	1		1				
<i>Galium triflorum</i>	15	7.5	1	15					
<i>Houstonia serpyllifolia</i>	9	4.5	1	7	1	1			
<i>Hypericum graveolens</i>	1	0.5	1		1				
<i>Impatiens pallida</i>	9	6.6	7.8	1	9	1			
<i>Isopyrum biternatum</i>	8	1.6	4.8	1	8				
<i>Juncoides echinatum</i>	5	2.5	3						
<i>Maianthemum canadense</i>	2	1.6	1.8	3					
<i>Oxalis acetosella</i>	59	96.6	92.8	1	49	46	27	15	2
<i>Prenanthes altissima</i>	9	4.5	6	1	2				
<i>Saxifraga leucanthemifolia</i>	8	1.6	4.8	8	1				
<i>Solidago glomerata</i>	3	23.3	13.2	1	3	6	5	2	
<i>Streptopus roseus</i>	2	16.6	9.3	4	5	2			
<i>Tiarella cordifolia</i>	47	46.6	46.8	2	50	18	3		2
<i>Trautvetteria carolinensis</i>	3	1.5	3			3			
<i>Urtica dioica</i>	3	1.5	2	1					
<i>Veratrum viride</i>	1	0.5	1		1				
<i>Veronica officinalis</i>	1	0.5	1		1				
<i>Viola</i> spp.....	3	3.3	3.2	5					
<i>Zizia Bebbii</i>	1	0.5	1		1				
Moss and lichen cover.....	94	96.6	94.8	20	26	37	44	46	

¹Based on 32 quadrats 10 by 20 meters, 20 in Stand A and 12 in Stand B.

²Based on 32 quadrats 5 by 5 meters, 20 in Stand A and 12 in Stand B.

³Pteridophytes and herb data based on 160 quadrats 1 by 1 meter, 100 in Stand A and 60 in Stand B.

maple. The stratification-coverage diagrams (Fig. 12) show the approximate vertical extent of each layer as well as surface extent (coverage). The understory and shrub layers show less coverage in Stand A than in Stand B, while the herb and ground layers are similar in both stands.

TREE LAYER

As shown in the stratification-coverage diagrams for the spruce-fir community (Fig. 12) the superior tree layer reaches a height of 90 feet in Stand A and only 60 feet in Stand B with about equal coverage for each stand. The superior layer is dominated by *Picea rubra* and *Abies Fraseri* at lower altitudes and by *Picea rubra*, *Abies Fraseri*, and *Betula lutea* at higher altitudes. In Stand A the inferior tree layer reaches a height of about 40 feet and covers about one fourth of the area. In Stand B this layer reaches a height of about 20 feet but covers approximately half the area.

Frequency.

Of the 8 tree species composing the spruce-fir community, *Picea rubra*, *Abies Fraseri*, and *Betula lutea* show frequencies of 80 percent or above for either stand, the first two running above 95 percent for the community (Table 9). *Acer spicatum*, frequency 50 percent, and *Sorbus americana*, frequency 20

percent, are more frequent at the upper altitudes. *Aesculus octandra*, frequency 6.2 percent, belongs to the beech-maple community, while *Prunus pennsylvanica*, frequency 2.5 percent, is a secondary successional species. Six of the 8 species occur in both stands.

Species characteristic of the tree layer, in order of frequency, are *Picea rubra*, *Abies Fraseri*, *Betula lutea*, *Acer spicatum*, and *Sorbus americana*. The first three are overstory species while the last two are understory species, although *Betula lutea* may occur in either layer.

TABLE 10. Comparison of basal area and density of trees in two stands of the spruce-fir community. The upper number represents basal area and the lower represents number of trees per acre above 1 inch d.b.h. (Based on 32 quadrats 10 by 10 meters, 20 in Stand A and 12 in Stand B. Both stands on the north slope but Stand A is approximately 400 feet higher than Stand B.)

Stands:	Basal area per acre: Density			Percent of total	Average basal area per stem
	A	B	Community		
<i>Picea rubra</i>	181.94 303.00	100.58 155.00	141.26 229.00	57.5 26.9	.63
<i>Abies Fraseri</i>	50.84 549.00	64.37 525.00	57.62 537.00	23.5 62.3	.11
<i>Betula lutea</i>	22.4 51.00	63.31 55.00	42.68 53.00	17.4 6.2	.81
<i>Acer spicatum</i>	1.78 21.00	2.40 38.00	2.09 29.00	.0 3.1	.07
<i>Fagus grandifolia</i>	1.51 3.0076 2.00	.3 .2	.38
<i>Sorbus americana</i>28 4.00	.87 13.00	.58 8.00	.2 1.0	.07
<i>Aesculus octandra</i>01 1.00	.92 2.00	.46 2.00	.2 .2	.23
<i>Prunus pennsylvanica</i>03 1.00 1.00	.01 1.00	.0 .1	.01
Totals.....	258.46 933.00	232.45 789.00	245.45 961.00	100.00 100.00	

Density.

Stand A shows a total density per acre of 933 as compared to 789 trees in Stand B (Table 10). The species showing higher densities at the higher altitudes are *Betula lutea*, *Acer spicatum* and *Sorbus americana*, while those with higher densities at the lower altitudes are *Picea rubra* and *Abies Fraseri*. Of the total individuals in the community, 62.3 percent belong to *Abies* and 26.9 percent belong to *Picea*. All other species compose only 10.8 percent of individuals, *Betula lutea* being highest with 6.2 percent.

Four of the species, *Abies Fraseri*, *Picea rubra*, *Betula lutea*, and *Acer spicatum*, are represented in all five size classes as shown in Table 11. *Sorbus americana* occurs in four classes while each of the other three species occurs in only one or two size classes. As *Sorbus americana* is usually a small tree, it would not be expected to appear in the large class of 10 inches d.b.h. or over. Since it appears in all other size classes, it is included as one of the four species which maintain themselves in the community.

TABLE 11. Density per acre of tree species by five size classes as represented in the spruce-fir community. (Trees above 1 inch d.b.h. based on 32 quadrats 10 by 20 meters; trees below 1 inch d.b.h. based on 32 quadrats 5 by 5 meters.)

Species	Number of individuals per acre					Total density
	Up to 1 ft. high	1 ft. high-1 in. d.b.h.	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. and over	
<i>Abies Fraseri</i>	832	1,040	399	112	24	2,407
<i>Picea rubra</i>	464	375	101	56	71	1,067
<i>Betula lutea</i>	384	230	18	8	26	666
<i>Acer spicatum</i>	136	240	24	4	1	405
<i>Sorbus americana</i>	40	155	6	2	203
<i>Fagus grandifolia</i>	1	1	2
<i>Aesculus octandra</i>	1	1	2
<i>Prunus pennsylvanica</i>	1	1
Totals	1,856	2,040	551	182	124	4,753

Tables 11 and 12 show clearly that most of the large trees belong to *Picea rubra* but *Abies Fraseri* is more important than *Picea rubra* in the 4 to 9 inch d.b.h. class. It is quite common to find *Abies* appearing in almost pure "pole" stands less than 4 inches d.b.h. which accounts for its relatively high basal area in this size class. Due to heavy density of these stands, they may better withstand high wind velocities. *Betula lutea* is most important as a larger tree, often reaching a d.b.h. of more than 24 inches.

TABLE 12. A comparison of basal area per acre of trees (1 inch d.b.h. and above) of the spruce-fir community by three size classes. (Based on 32 quadrats 10 by 20 meters.)¹

Species	Basal area per acre			
	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. and over	Total
<i>Picea rubra</i>	3.22	14.66	123.38	141.26
<i>Abies Fraseri</i>	13.86	20.69	23.07	57.62
<i>Betula lutea</i>42	2.82	39.44	42.68
<i>Acer spicatum</i>80	.96	.33	2.09
<i>Fagus grandifolia</i>14	.62	.76
<i>Sorbus americana</i>32	.2658
<i>Aesculus octandra</i>46	.46
<i>Prunus pennsylvanica</i>0101
Totals	18.63	39.53	187.30	245.46
Percentage of total basal area	7.6	12.0	80.4	100.

¹Basic figures from 32 quadrats 10 by 20 meters were used to determine actual basal areas for each size class. These numbers were reduced to an acre basis.

Basal Area.

A much better idea of degree of dominance may be gained by referring to the first set of figures in Table 10, which represents basal area. Stand A has a basal area of 258.46 square feet per acre while Stand B has 232.45 square feet per acre. It appears to be a better site than Stand B for *Picea rubra*, but apparently not as good for *Abies Fraseri* as Stand B. *Betula lutea* shows about three times as great a

basal area in Stand B as in Stand A. Tolerance of *Picea* to strong winds is one important explanation since wind action is more severe on the higher slopes. Of the total basal area, *Picea rubra* represents 57.5 percent, *Abies Fraseri*, 23.5 percent, *Betula lutea*, 17.4 percent, and all other species less than 1 percent each. *Betula lutea* shows the largest average stem size with a mean basal area of 0.81 square feet. *Picea rubra* ranks second with 0.63 square feet per stem while *Abies Fraseri* ranks third with only 0.11 square feet per stem.

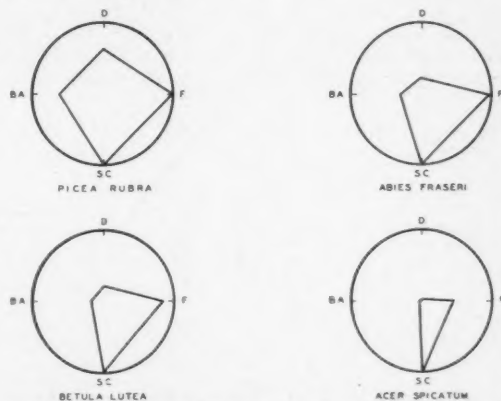


FIG. 13. Phytophotographs of the important tree species of the spruce-fir community. Constructed from data presented in Table 14. Legend is the same as for Fig. 8.

Phytophotographs.

Phytophotographs (Fig. 13) show graphically relative value of the four most important trees of this community. *Picea rubra* ranks highest in the number of

TABLE 13. Data upon which phytophotographs in Figure 13 are based. (All values are on a percentage basis and are taken from Tables 10, 11, and 12.)

Species	Radius 1: Density 10 in. d.b.h. and over	Radius 2: Frequency 1 in. d.b.h. and over	Radius 3: Number of size classes	Radius 4: Basal area
<i>Picea rubra</i>	57.3	100	100	57.5
<i>Abies Fraseri</i>	19.4	96.8	100	23.5
<i>Betula lutea</i>	21.0	84.3	100	17.4
<i>Acer spicatum</i>9	43.7	100	.9

large trees, in frequency percentage of trees, and in basal area. *Abies Fraseri* ranks second but has fewer trees above 10 inches d.b.h. than *Betula lutea*, which occupies third place. *Acer spicatum* ranks lowest, representing only 0.9 percent of the trees 10 inches d.b.h. or over and has an insignificant basal area. However, since it shows high frequency and is present in all size classes, it is an important species in the community.

SHRUB LAYER

Frequency.

As shown in Table 9 the three shrubs with highest frequencies are *Vaccinium erythrocarpum*, 45.9 per-

cent; *Viburnum alnifolium*, 37.5 percent, and *Rhododendron catawbiense*, 35 percent. *Viburnum* is more frequent at lower altitudes while the other two are more frequent at higher altitudes.

All other species have a frequency below 10 percent except *Cornus alternifolia*, 14.2 percent. All species occurred in Stand A except *Rubus canadensis* which is usually confined to openings. *Hydrangea arborescens*, *Sambucus racemosa*, and *Lonicera canadensis* are rare shrubs of this area and are confined to upper altitudes.

TABLE 14. Density of woody species under 12 feet high by three height classes as found in the spruce-fir community. (Based on 32 quadrats 5 by 5 meters each.)¹

Species	Number per acre				Coverage Class
	0-1 ft.	1-3 ft.	3-12 ft.	Total	
Trees					
<i>Abies Fraseri</i>	832	500	540	1,872	1
<i>Picea rubra</i>	464	195	80	739	1
<i>Betula lutea</i>	384	50	180	614	1
<i>Acer spicatum</i>	136	65	175	376	1
<i>Sorbus americana</i>	40	25	15	80	1
Shrubs					
<i>Rhododendron catawbiense</i>	145	145	145	435	1
<i>Vaccinium erythrocarpum</i>	100	120	45	265	1
<i>Viburnum alnifolium</i>	10	70	100	180	1
<i>Rubus canadensis</i>	25	40	65	0
<i>Cornus alternifolia</i>	10	35	45	0
<i>Ribes rotundifolium</i>	35	35	0
<i>Lonicera canadensis</i>	10	15	25	0
<i>Hydrangea arborescens</i>	10	10	0
Total tree individuals	1,856	835	990	3,681	
Total shrub individuals	300	470	290	1,060	
Total woody individuals	2,156	1,305	1,280	4,741	

¹The basic figures for seedlings under 6 inches were taken from 160 quadrats 1 by 1 meter and reduced to acre basis.

Density.

Of 4,741 woody individuals less than 12 feet high (Table 14), occurring in the shrub layer, 3,681 or 77.6 percent are individuals of tree species. These transgressives include 1,872 *Abies Fraseri*, 739 *Picea rubra*, and 614 *Betula lutea*. The density per acre for each of the more common shrub species is as follows: *Rhododendron catawbiense*, 435; *Vaccinium erythrocarpum*, 265; and *Viburnum alnifolium*, 180. The other 5 shrub species are represented by a total of only 180 individuals.

Frequency, coverage, and density data show that *Rhododendron catawbiense*, *Vaccinium erythrocarpum*, *Viburnum alnifolium*, *Cornus alternifolia* and *Ribes rotundifolium* are the more important species occurring in the shrub layer of the spruce-fir community.

HERB LAYER

Frequency.

Of the 5 pteridophytes present in the herb layer, only 3 may be considered characteristic. They are *Dryopteris dilatata*, frequency 84.1 percent, *Lycopodium lucidulum*, frequency 31.5 percent, and *Polypodium virginianum*, frequency 20.8 percent.

Athyrium asplenoides is confined to moister sites of the upper slopes while *Polystichum acrostichoides*, an accidental species, belongs to the beech-maple and oak-chestnut communities of lower altitudes.

Of the 39 species occurring in the herb layer, *Oxalis acetosella* is the most frequent herb and is present in 92.8 percent of the quadrats. Other of the more frequent species are: *Tiarella cordifolia*, 46.8 percent; *Aster divaricatus*, 36 percent; *Chelone Lyoni*, 19 percent; *Circaea alpina*, 17.5 percent; *Aster acuminatus*, 17 percent; *Clintonia borealis*, 16.2 percent; and *Solidago glomerata*, 13.2 percent. These occur in each stand and are the most characteristic herb species of the community. All of the other 26 species have frequency indices below 10, and 7 are below 1.

Coverage.

The distribution of coverage classes for each species of the herb layer is shown in Table 9. *Dryopteris dilatata* and *Oxalis acetosella* belong to coverage class 2. They cover about 50 percent of the stand which is a greater coverage than that of all other species of the herb layer combined. No other species shows more than 6 percent coverage. *Aster acuminatus* and *Aster divaricatus* occur with coverages up to class 3 and 4, respectively, but more frequently occur with coverages of class 1 or 0. As might be expected, species with high frequency indices show greater distribution in the coverage classes. There also appears a positive correlation between frequency index and total coverage of species which emphasizes the value of frequency data in describing the organization and structure of a community.

Woody Seedlings.

All seedlings of woody species taken together cover about 3 percent of the total area sampled. *Abies Fraseri* and *Picea rubra* were more frequent than all other species combined but neither species covered more than 25 percent of any quadrat. *Viburnum alnifolium* and *Sorbus americana* were each recorded once for class 3; however, seedlings of either were rarely seen. As would be expected, no coniferous seedlings were observed in heavy shade. Seedlings of the two dominants, *Abies* and *Picea*, are most frequent, showing 18.7 percent and 15 percent, respectively.

MOSS LAYER

Table 9 shows that mosses and lichens occur in 94.8 percent of the herb plots under the coniferous forest and cover about 65 percent of total ground area. Moss often covers tree trunks to a height of a yard or two and *Usnea* sp. is commonly seen hanging from the limbs of trees.

COMMUNITY AS A WHOLE

This forest community, which commonly occurs in the Southern Appalachians above 4,500 feet, is classified by the Society of American Foresters (1932) as Forest Cover Type 19, red spruce-southern balsam fir. It is further described as commonly having yellow



FIG. 14. Interior view of spruce-fir forest as represented by Stand B. Note large spruce trees with long straight boles and abundant reproduction of both spruce and fir. *Viburnum* and *Dryopteris* are seen in foreground.

birch and hemlock associated with the dominants, especially at the lower portions of its range. No hemlock was observed on Roan Mountain above 4,000 feet, spruce and fir being the only conifers present in the area under study. From basal area studies yellow birch is about three times as important at 4,500-5,900 feet as at an altitude 500 feet lower.

Frequency class diagrams (Fig. 6) show the spruce-fir community to be more homogeneous than the beech-maple community, since the former has more of its species in the higher frequency classes. The upper portion of the spruce-fir community (Stand B) shows greater homogeneity than the lower portion (Stand A). Both frequency class curves (histograms) compare favorably with the "normals" of Raunkiaer and Kenoyer (Cain, 1932). When the two stands are combined, there appears less homogeneity than when they are viewed separately. Only 38 species occur in Stand B as compared to 50 species for Stand A. Most of the extra species in Stand A are accidental species from other communities, as *Fagus grandifolia*, *Polystichum acrostichoides*, and *Cimicifuga racemosa* from the beech-maple forest below and *Veronica officinalis* and *Houstonia serpyllifolia* from the grassy balds above. *Prunus pennsylvanica*, *Sambucus racemosa* and *Hypericum graveolens* are secondary successional species. This variation in floristic composition is reflected in the frequency class diagrams.

The spruce-fir community is characterized by four layers, a tree layer, a shrub layer, an herb layer, and a ground layer. The tree layer may be further divided into superior and inferior layers. The tree layer, consisting of 8 species, is dominated by *Picea rubra* and *Abies Fraseri* in the superior layer, and by *Betula lutea* and *Acer spicatum* in the inferior layer, birch appearing as one of the dominants at higher altitudes. The superior tree layer covers about 0.6 of the stand and the inferior layer covers about 0.4. The tree layer as a whole covers about 0.9. The

shrub layer, consisting of 9 species, is dominated by *Rhododendron catawbiense*, *Vaccinium erythrocarpum*, and *Viburnum alnifolium* and covers about one half of the ground area. The herb layer, which covers about three fourths of the ground surface, consists of 39 species. It is dominated by *Dryopteris dilatata* in the upper stratum and by *Oxalis acetosella* nearest the ground. Important associated species in order of frequency are: *Tiarella cordifolia*, *Aster divaricatus*, *Aster acuminatus*, *Clintonia borealis*, *Solidago glomerata*, *Lycopodium lucidulum*, and *Polypodium virginianum*. The ground layer is carpeted with mosses and closely associated with them is *Oxalis* of the herb layer. *Usnea* which hangs from limbs of many trees throughout the community gives evidence of a constantly humid atmosphere under the spruce-fir canopy.

BALD COMMUNITIES

More or less extensive bald areas are characteristic of higher summits of the Southern Appalachians. They have been mentioned or briefly described by botanists since the days of Michaux and Gray. In more recent years plant ecologists have become much interested in these "sub-alpine" areas as indicated by the writings of Harshberger (1903), Cain (1930), Davis (1930), Camp (1931) and Wells (1932, 1937). Most of the recent interest, however, has been shown in an attempt to explain the origin rather than to determine the structure and composition of such communities. The present study deals with both interests, since each helps to explain the other.

In order to present an adequate picture of the structure and composition of the high bald communities of Roan Mountain, data were recorded from 450 quadrats located in 16 different stands. The stands were well distributed throughout the full extent of the areas occupied by these communities. The dynamics of the communities will later be discussed under "Succession."

A grassy bald community occupies about one half of the total bald area on Roan Mountain, and is considered by Wells (1937) to be perhaps the largest high mountain grassy bald of the Southern Appalachians. On the remaining portion, the rhododendron bald community is somewhat more extensive than the alder bald community. In certain protected areas of the Round Bald, dwarfed trees appear in the grass area in an "orchard" condition, *Crataegus* and *Aesculus* appearing on the southwest slope and *Aesculus* on the northeast slope. A dense stand of browsed beech often borders the lower margin of this community on Round Bald, while rhododendron thicket or spruce-fir forest border the grassy stretches on the mountain summit.

GRASSY BALD COMMUNITY

Location and Description of Stands.

By far the best development of the grassy bald community is on Round Bald, a dome-shaped summit immediately east of Carvers Gap. This community is often referred to as "mountain meadow" or "sub-



FIG. 15. Round Bald (grass) as it appears from west side. Carvers Gap is seen in front center. Stands A, B, and C were located on this exposure. Note dwarfed *Crataegus* above and to the south (right) of Carvers Gap and the patch of *Alnus* to the upper right immediately above the Fagus.

alpine meadow." Stands A, B, C, D, and E were located on this bald between 5,500 and 5,700 feet altitude. The exposures of these stands were as follows: Stand A, northwest; Stand B, southwest; Stand C, west; Stand D, north; and Stand E, southeast. Stand F was about 1.25 miles east of Carvers Gap on the northeast slope of Jane Bald at an altitude of about 5,700 feet. Stand G was approximately 2



FIG. 16. Looking east across Stand E which is located on the southeast slope of Round Bald. This represents best development of *Danthonia* on Roan Mountain. August, 1936.

miles west of Carvers Gap and 250 yards southwest of Cloudland Lodge at 6,150 feet. These stands were located on areas varying from almost level in Stand G to as much as a 30 degree slope in the steeper portion of Stand E. The average slope for the community is about 10 degrees.

Wind velocities are medium to strong in all stands, being strongest in Stand D, which is fully exposed to the prevailing northerly winds, and lightest in Stand G, which is best protected.

HERB LAYER

Frequency.

The frequency percentage and mean coverage class for each species recorded from the quadrats are shown in Table 15. The three species belonging to Class E (8 to 100 percent) for the community are *Danthonia compressa*, *Rumex acetosella*, and *Agrostis hyemalis*. *Danthonia* occurred in every quadrat of every stand except in Stand D of the north slope where it was absent from 2 quadrats. The mean community frequency for this species is 99.4 percent. *Rumex acetosella* varies from 72 percent frequency in Stand F to 98 percent frequency in Stand C and shows a mean frequency of 90.3 percent. *Agrostis hyemalis* ranges from 60 percent in Stand E to 100 percent in Stand D, averaging 87.4 percent frequency for the community. *Fragaria virginiana*, frequency 65.1 percent, is the only species in Class D, and ranges from 10 percent in Stand C to 100 percent in Stand E. The mean community frequency percentages for species of Class C are: *Houstonia serpyllifolia*, 44.8 percent, and *Carex flexuosa*, 41.1 percent. Class B is represented by 4 species: *Juncus tenuis*, 40 percent; *Viola blanda*, 33.8 percent; *Potentilla canadensis*, 26.3 percent; and *Carex glaucoidea*, 22.9 percent. Of the 20 species in Class A, only two are above 10 percent, *Poa pratensis*, 11.6 percent, and *Veronica officinalis*, 14 percent.

The 7 species present in all 7 stands are: *Danthonia compressa*, *Rumex acetosella*, *Agrostis hyemalis*, *Fragaria virginiana*, *Carex flexuosa*, *Carex glaucoidea*, and *Veronica officinalis*. The 4 species occurring in 6 of the 7 stands are: *Agrostis alba*, *Houstonia serpyllifolia*, *Poa pratensis*, and *Potentilla canadensis*.

Coverage.

The distribution of coverage classes for each species is shown in Table 15. There is only one dominant species in the herb layer, *Danthonia compressa*, which covers from 50 to 75 percent of the total area. It rarely covers less than 25 percent of the surface of any quadrat and frequently covers more than 75 percent of the surface of some quadrats, especially in areas of better development where it often attains a height of 2 feet. Of the other 29 species present in the herb layer, only 5 cover as much as 5 percent of the surface. These are *Rumex acetosella*, *Fragaria virginiana*, *Carex flexuosa*, *C. lucorum*, and *Agrostis hyemalis*.

Woody Seedlings.

As previously indicated, there are no trees or shrubs present in typical grassy bald areas. None taller than a foot were seen within the boundaries of the 7 stands studied. Seedlings recorded from the 250 quadrats are as follows: 8 *Rhododendron catawbiense*, 2 to 4 inches high; 6 *Picea rubra*, 2 to 10 inches high; and 1 *Vaccinium erythrocarpum*, 4 inches high. Of these 15 seedlings, 12 were present in Stand G which is bounded on either end by *Rhododendron catawbiense* and is within 100 meters of the coniferous forest which serves as a wind-break to the area.

TABLE 15. Frequency and coverage data for species of the grassy bald community. Where two numbers occur opposite a species, the upper number represents frequency percentage and the lower number represents coverage class. (Based on 250 quadrats, 1 by 2 meters, August, 1936.)

Floristic list	Frequency percent and coverage class							Com- muni- ty 250 ...	Distribution of coverage classes for the community					
Stand: No. of samples: Altitude: Exposure: Slope:	A 50 5,500 NW 7°	B 25 5,500 SW 7°	C 50 5,600 W 8°	D 50 5,650 N 10°	E 25 5,700 SE 15°	F 25 5,700 NE 7°	G 25 6,150 S 5°		0	1	2	3	4	5
Pteridophytes														
<i>Dryopteris dilatata</i>	4			6		4	2.0	6						
	0			C		0	0							
Herbs														
<i>Achillea millefolium</i>		4					.6	1						
		0					0							
<i>Agrostis alba</i>	4		10	8	32	12	8	10.6	30	2				
	0		0	0	1	0	0	0						
<i>Agrostis hyemalis</i>	98	88	98	100	60	96	72	87.4	154	68	5			
	0	0	0	1	0	1	0	1						
<i>Carex brunneascens</i>	2						.3	1						
	0						0							
<i>Carex flexuosa</i>	2	4	66	64	24	32	96	41.1	35	62	13	3		
	0	0	1	1	0	0	1	1						
<i>Carex glaucoidea</i>	2	4	22	20	76	28	8	22.9	45	4				
	0	0	0	0	0	0	0	0						
<i>Carex lucorum</i>	2	4	10		20		5.1	5	2	3	5	1		
	0	0	1		2		1							
<i>Cerastium semidecandrum</i>				4		8	1.7	4						
				0		0	0							
<i>Danthonia compressa</i>	100	100	100	96	100	100	100	99.4		4	22	85	67	70
	4	4	4	3	4	3	5	4						
<i>Fragaria virginiana</i>	74	100	10	24	100	88	60	65.1	71	41	21	7	1	
	1	2	0	0	1	1	0	1						
<i>Hieracium gronovii</i>		4	2				.9	2						
		0	0				0							
<i>Holcus lanatus</i>					4		.6	1						
				0			0							
<i>Houstonia serpyllifolia</i>	86		22	20	16	80	88	44.8	85	22	4			
	0		0	0	0	0	1	0						
<i>Juncoides echinatum</i>						4	12	2.3	4					
						0	0	0						
<i>Juncus tenuis</i>	38	96	74	44	4	20	4	40	101	7	2			
	0	0	0	0	0	0	0	0						
<i>Phleum pratense</i>							4	.6	1					
							0	1						
<i>Phytolacca decandra</i>			4				.6	2						
			0				0							
<i>Poa pratensis</i>	2	32	4		32	36	4	15.7	27	1	1			
	0	0	0		0	0	0	0						
<i>Potentilla canadensis</i>	16	36		2	84	20	36	26.3	27	26				
	0	0		0	0	0	0	0						
<i>Potentilla monspeliensis</i>					8	4	1.7	1	2					
					0	0	0							
<i>Potentilla tridentata</i>							16	2.3		1	1	2		
							1	0						
<i>Rumex acetosella</i>	96	96	98	90	92	72	88	90.3	148	77	3	1		
	1	0	1	1	0	0	0	1						
<i>Trisetum virginianum</i>					4	4	1.1	3						
					0	0	0							
<i>Trifolium hybridum</i>					4		.6	2						
					0		0							
<i>Trifolium saxicola</i>			8			28	4	5.4	11	1				
			0			0	0	0						
<i>Veronica officinalis</i>	20	12	10	20	4	12	12	12.9	29	4				
	0	0	0	0	0	0	0	0						
<i>Veronica serpyllifolia</i>					4		.6	1						
					0		0							
<i>Viola blanda</i>	38	48		38	44	60	40	33.8	94	1				
	0	0		0	0	0	0	0						
<i>Viola cucullata</i>	4	8					1.7	4						
	1	0					0							
Miscellaneous														
<i>Polytrichum commune</i>	98	100	98	100	40	96	96	92.4	63	46	40	50	27	5
	3	0	2	2	0	2	1	2						
Mosses and lichens (other than <i>P. commune</i>)	20	8	2	2			4.6	13	1					
		0	0	0			0							

Heavy migration of seeds from nearby parent plants and protection against high wind velocities best explain presence of woody seedlings in this stand.

GROUND LAYER

The ground layer is composed of several mosses and lichens, but is dominated by *Polytrichum commune* which covers more than ten times the combined areas shaded by all other species present in this layer.

Moss is not conspicuous in the area except as occasional "hummocks," but the study shows that *Polytrichum commune* is present in every stand and shows a frequency of 92.4 percent for the community. The frequency is above 80 percent for all stands except Stand E, on the southeast slope, which shows only 40 percent frequency but has the best development of *Danthonia compressa* of any stand. This better development of *Danthonia* may indicate a drier site, which is less favorable to the mesic *Polytrichum*. It is closely interwoven between bases of grass and sedge culms, and is so uniform in its distribution that high frequencies would result even though quadrats were very small.

The highest coverage for *Polytrichum* is in Stand A where it covers 25 to 50 percent of the surface (class 3). The average for the community is about 10 percent (class 2).

Lichens and mosses other than *Polytrichum* occurred in 4 of the 7 stands with a mean frequency of 4.6 percent. Average coverage for all such plants is less than 1 percent for the community, and did not exceed 3 percent for any quadrat.

COMMUNITY AS A WHOLE

An examination of the Frequency Class Diagrams (Fig. 17) shows that the grassy bald community is much more homogeneous floristically than either of the forest communities studied (Fig. 6). The individual stands show even greater homogeneity. There are 30 species listed for the herb layer of this community, but not more than 18 occur in any one of the 7 stands. The species with high frequencies also tend to be present in all stands while the species with low frequencies tend to be present in few of the stands. About half of the floristic list represents species which have been introduced into the area, principally by grazing animals. These species become locally established and usually show low frequencies and coverages. (*Rumex*, of high frequency, is a notable exception.) On the other hand, the native species tend to show

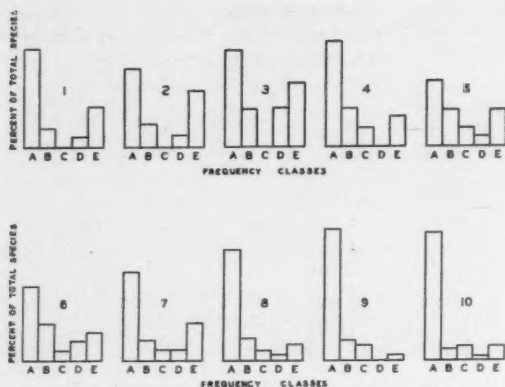


FIG. 17. Frequency class diagram for bald communities of Roan Mountain.

1. Stand A of grassy bald.
2. Stand B, same.
3. Stand C, same.
4. Stand D, same.
5. Stand E, same.
6. Stand F, same.
7. Stand G, same.
8. Community as a whole.
9. Rhododendron bald community.
10. Alder bald community.

uniformity of distribution throughout the community. A rather uniform physiognomy results, except for occasional small areas dominated by moss hummocks.

Characteristic species are *Houstonia serpyllifolia*, *Carex flexuosa*, *Carex glaucoidea*, *Potentilla tridentata*, and *Viola blanda*.

Conspicuous introduced species present in the community are: *Achillea millefolium*, *Agrostis alba*, *Carex brunnescens*, *Cerastium semidecandrum*, *Hieracium Gronovii*, *Holcus lanatus*, *Phleum pratensis*, *Phytolacca decandra*, *Poa pratensis*, *Trifolium hybridum*, *Veronica serpyllifolia*, and *Veronica officinalis*.

RHODODENDRON BALD COMMUNITY

The rhododendron bald community of Roan Mountain, known to the general public as the "Rhododendron Gardens," has been reported as covering about 600 acres—a probable overestimate.⁵ The best development of this community occurs along the flattened summit between Cloudland and Roan High Bluff at 6,000 to 6,150 feet altitude. Most of the area occupied by the community is on the southeast side of the divide (Fig. 19). This community is almost surrounded by the spruce-fir forest and is interrupted by patches of grassland of varying extent.

Location of Stands.

Four areas were selected as stands located as follows: Stands A and B at the northwest end of area

⁵ No attempt has been made to determine the exact area covered by this community, but based on general estimates, there appears to be less than 200 acres. The 600-acre estimate was made for advertising purposes. If the total area in which rhododendron occurs is considered, including the spruce-fir forest, the 600-acre estimate is not too high.

immediately south of the divide and with a south-eastern exposure (Fig. 19); Stand C about 400 meters northeast of Stand A and about 300 meters south of the divide, with a southern exposure; Stand D immediately across the divide from Stand B and with a northwest exposure. Each of these stands was at approximately 6,100 feet altitude and on land that varied in slope from 2 to 10 degrees. Wind velocities were medium to strong in Stand D but mild to brisk in other stands, being lowest in Stand B.

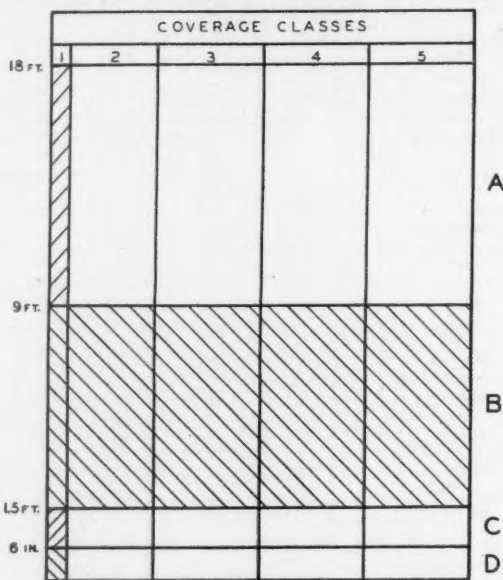


FIG. 18. Cover-stratification diagram for heath bald community.

- A. Tree layer of *Picea*, *Abies*, and *Sorbus*.
- B. Shrub layer, an almost pure stand of *Rhododendron catawbiense*.
- C. Herb layer, suppressed *Dryopteris*, *Houstonia*, *Viola*, and *Carex*.
- D. Ground layer of mosses and lichens.

LAYERS

Shrub, herb, and ground layers are represented in the rhododendron bald community (Fig. 18), but only the shrub layer shows more than 5 percent coverage. A few individuals of *Picea rubra* and *Sorbus americana* overtop the shrub canopy, suggesting a tree layer (Fig. 18). Due to the heavy opaque nature and arrangement of rhododendron leaves which shade more than 95 percent of the surface, very little light reaches the ground. This factor, added to the fact that *Rhododendron catawbiense* produces a network of feeder roots in the upper 2 inches of soil, excludes many individuals which might otherwise be present in the herb layer. A layer of dead leaves not yet decayed covers the ground and retards development of moss. For practical purposes, and upon superficial examination, one might say that there is no herb layer and only a very weak ground layer. Thus the rhododendron bald is essentially a one-layered community.

SHRUB LAYER

Frequency.

Frequency and coverage data are presented in Table 16. *Rhododendron catawbiense* shows a frequency of 100 percent in each stand. *Alnus alnobetula* ranks second, showing a frequency of 13 percent for the community and was present in 3 of the 4 stands. *Picea rubra*, usually a "transgressive," ranks next with 8 percent frequency and was present in all stands. *Ribes rotundifolium* was in 3 stands and shows 3 percent frequency. *Leiophyllum Lyoni*, *Sambucus racemosa*, and *Vaccinium erythrocarpum* were present in half the stands and each shows a frequency of 5 percent or less. Each of the remaining 5 species was present in only one quadrat of one stand, thus showing a frequency of 1 percent each.

TABLE 16. Frequency and coverage data for species present in the rhododendron bald community. Where two numbers occur opposite a species, the upper number represents frequency percentage and the lower number represents coverage class. (August, 1934.)

Floristic list	Frequency percent and coverage					Distribution of coverage classes for the community				
Stand:.....	A	B	C	D	Community					
No. of samples:.....	25	25	25	25	100					
Altitude:.....	6,050	6,100	6,150	6,100						
Exposure:.....	SE	SE	S	NW						
Slope:.....	6°	8°	5°	7°						
Trees										
<i>Abies Fraseri</i>			4		1			1		
			0		0					
<i>Picea rubra</i>	4	8	4	16	8		2	2	1	2
	0	1	0	1	1					
<i>Sorbus americana</i>		4			1		1			
		0			0					
Shrubs										
<i>Alnus alnobetula</i> ..	1	24	8	20	13		7	5		
		1	0	1	1					
<i>Leiophyllum lyoni</i> ..	4	4			2	1	1			
	0	0			0					
<i>Menziesia pilosa</i> ..	4				1	1				
	0				0					
<i>Pyrus melanocarpa</i> ..		4			1		1			
		0			0					
<i>Rhododendron catawbiense</i>	100	100	100	100	100			1	1	96
	5	5	5	5	5					
<i>Ribes rotundifolium</i> ..	4		4	4	3		1	1	1	
	0		0	0	0					
<i>Sambucus racemosa</i>	8	12			5		3	2		
	0	0			0					
<i>Vaccinium corymbosum</i>		4			1		1			
		0			1					
<i>Vaccinium erythrocarpum</i>		4	8		3	1	2			
		0	0		0					
Peridophytes										
<i>Dryopteris dilatata</i>	84	44		48	44	42	2			
	0	0		0	0					
<i>Lycopodium lucidulum</i>				8	2	2				
				0	0					
<i>Lycopodium selago</i>				4	1	1				
				0	0					
Herbs										
<i>Agrostis perennans</i>		8	12		5	5				
		0	0	0	0					
<i>Aster acuminatus</i>		4			1	1				
		0			0					
<i>Carex flexuosa</i>	52	64	72	28	54	54				
	0	0	0	0	0					

TABLE 16 (Continued)

Floristic list	Frequency percent and coverage					Distribution of coverage classes for the community				
Stand:.....	A	B	C	D	Community					
No. of samples:.....	25	25	25	25	100					
Altitude:.....	6,050	6,100	6,150	6,100						
Exposure:.....	SE	SE	S	NW						
Slope:.....	6°	8°	5°	7°						
<i>Carex laxiflora</i>	4	8			3	2				
	0	0			0					
<i>Carex leptalea</i>		16			4	4				
		0			0					
<i>Circaea alpina</i>	24	16	4		11	9	2			
	0	0	0		1					
<i>Danthonia compressa</i>	4		8	4	4	4				
	0		0	0	0					
<i>Deschampsia flexuosa</i>	28	8	24	24	21	21				
	0	0	0	0	0					
<i>Erechtites hieracifolia</i>	4				1	1				
	0				0					
<i>Eupatorium roanensis</i>				4	1	1				
				0	0					
<i>Galium triflorum</i>	4				1	1				
	0				0					
<i>Houstonia purpurea</i>	4				1	1				
	0				0					
<i>Houstonia serpyllifolia</i>	60	44	52	24	45	41	4			
	0	0	0	0	0					
<i>Juncoides echinatum</i>	28	24	28	8	22	21	1			
	0	0	0	0	0					
<i>Maianthemum canadense</i>	12	4	24	52	23	23				
	0	0	0	0	0					
<i>Phytolacca decandra</i>	16	4	4		6	6				
	0	0	0		0					
<i>Rumex acetosella</i>		8	12		5	5				
		0	0		0					
<i>Steironema sp.</i>				4	1	1				
				0	0					
<i>Trautvetteria carolinensis</i>	52			12	16	15	1			
	0			0	0					
<i>Veronica officinalis</i>		8			2	2				
		0			0					
<i>Viola sp.</i>	28	60	32	28	37	35	2	1	1	
	0	0	0	0	0					
Miscellaneous										
Moss and lichen cover.....	96	80	84	84	86	63	21	1	1	
	1	1	1	1	1					

Coverage.

Rhododendron catawbiense shows a mean coverage of class 5 for the community. Except for occasional small openings between clumps, this species completely shades the ground. *Picea* and *Alnus* are the only other species that cover more than 1 percent of the surface, these two species covering about 2 percent of the surface, respectively (class 1).

Density.

Of the 314 woody plants on 400 square meters actually sampled, 242, or 77.1 percent, were *Rhododendron*. More than half of the remaining individuals were *Alnus*, *Ribes*, and *Picea* (Table 17). Of the 5,142 canes present, 5,021, or 97.6 percent, were *Rhododendron* canes. The spacing between canes of this species averaged 28 centimeters (11 inches). The average diameter of the canes at 1 foot above ground was slightly less than 1 inch. So dense is the thicket produced by these canes that it is possible to move through a typical stand only with difficulty. There were 17 times as many clumps of *Rhododendron* as

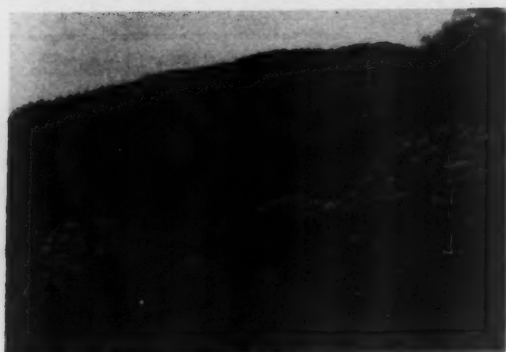


FIG. 19. A portion of "rhododendron garden," looking westward. Stands A and B were located in area beyond first group of conifers. Note that conifers pierce shrub canopy. A *Sorbus americana* appears to the right. Altitude, 6,100 feet. June 25, 1935.

of *Alnus* and 80 times as many canes of the former as of the latter. The average distance between *Alnus* clumps was approximately 5 meters (14 feet). *Ribes* clumps showed about the same spacing as *Alnus*. The other 6 shrub species show very low densities.

Woody Seedlings.

Table 17 shows 617 *Rhododendron* seedlings under 6 inches high present on the 400 square meters sampled. It is interesting to note that no *Alnus* seedlings were recorded from the same area. *Ribes* seedlings were more numerous than all other shrub seedlings. Of the tree seedlings, *Sorbus americana* was most abundant, showing an average spacing of 1.8 meters (7.3 feet). Twelve *Picea* seedlings were recorded as compared to 7 individuals of this species which had pushed through the shrub canopy. This most significant dynamic indication will be discussed later.

HERB LAYER

Frequency.

The herb layer is represented by 3 pteridophytes and 21 herbs. The one fern present, *Dryopteris dilatata*, frequency 44 percent, occurred in 3 of the 4 stands. The 2 club mosses, *Lycopodium lucidulum* and *L. selago*, were present only on the north slope (Stand D), with a frequency of 8 percent and 4 percent, respectively.

Of the 21 herbs, *Carex flexuosa* and *Houstonia serpyllifolia* were the most frequent, showing 54 percent and 45 percent, respectively, being the only 2 species in Class C. Class B is represented by 4 species as follows: *Viola blanda*, 37 percent; *Maianthemum canadense*, 23 percent; *Juncoides echinatum*, 22 percent; and *Deschampsia flexuosa*, 21 percent. These 6 herb species are rather uniformly distributed within the different stands. It is an interesting coincidence that these 6 species are the only herb species present in all 4 stands. The species which occurred in only 3 stands were *Trautvetteria carolinensis*, frequency 16 percent; *Circaea alpina*, frequency 11 percent; *Phytolacca decandra*, frequency 6 percent; *Rumex*

TABLE 17. Density by height classes of woody species present in the rhododendron bald community. (Based on 100 quadrats, 2 by 2 meters. August, 1934.)

Shrub species	Clump	Canes per clump	Height in feet: number of canes										Total above 1/2 foot
			0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	
<i>Rhododendron catawbiense</i>	242	21617	1692	802	531	357	330	660	357	86	6		5021
<i>Alnus alnobetula</i>	14	5		18	4	14	7	7	13				63
<i>Ribes rotundifolium</i>	16	74		1				15					16
<i>Pyrus melanocarpa</i>	9				0								9
<i>Sambucus racemosa</i>	5	11	3					1	1				5
<i>Vaccinium corymbosum</i>	4			4									4
<i>Vaccinium erythrocarpum</i>	3		3										3
<i>Leiophyllum Lyoni</i>	2		2										2
<i>Menziesia pilosa</i>	1		1										1
Tree species													
<i>Picea rubra</i>	13	12	2	4							7		13
<i>Sorbus americana</i>	4	139	2	1							1		4
<i>Acer saccharum</i>		4											
<i>Abies Fraseri</i>		13											
<i>Betula lutea</i>	1	1									1		1
Totals	314	871	1005	829	545	371	337	683	358	99	6		95142

acetosella, frequency 5 percent; and *Danthonia compressa*, frequency 4 percent. Each of the remaining 11 species occurred in only 1 or 2 stands and show less than 5 percent frequency.

Coverage.

No species of the herb layer showed as much as class 1 coverage for any single stand or for the community (Table 16). There is a very poor distribution of species among the coverage classes. Only 8 species showed more than 1 percent coverage each in any quadrat (Table 16). Only 1 species, *Viola blanda*, showed more than 5 percent coverage in any quadrat, showing as high as class 3 (25 to 50 percent coverage) in one quadrat. No species showed as much as 1 percent coverage, unless it was present in an open area or at the edge of an opening.

GROUND LAYER

Mosses and lichens, principally mosses, show a frequency of 86 percent for the community. *Polytrichum commune*, characteristic of grassy balds, is common in the small openings and at the edge of openings while mosses characteristic of the spruce-fir forest are common on the bases of *Rhododendron* clumps and on the lower trunks of the few trees present. The distribution of coverage classes ranges up to class 3, but more quadrats show class 0. The

highest coverages are for quadrats located under the shade of conifers.

COMMUNITY AS A WHOLE

Since the rhododendron bald community consists of a practically pure stand of *Rhododendron catawbiense*, it shows an extremely uniform physiognomy (Fig. 19). Based on data presented in Tables 16 and 17, there is only one dominant for this community, *Rhododendron catawbiense*, which shows 100 percent frequency, presence in all stands, class 5 (75 to 100 percent) coverage, and 97.8 percent of the total density. There are a number of associated species in the herb layer which show low frequency, coverage, and density.

The community appears to be somewhat unstable, since the heavy and almost pure stand of *Rhododendron* shades a rather suppressed and depauperate herb layer and since the community is susceptible to invasion by conifers which break through the shrub layer and survive as a potential tree layer. There seem to be no strictly characteristic species of the herb layer in the sense of "exclusive" species. No species except *Viola blanda* shows sufficient vitality to reproduce itself under the shrub layer. Species of the herb layer thus appear to be ephemeral invaders from the grassy bald or from the spruce-fir forest.

So far as could be determined, this community represents the most interesting, unique, and extensive stand of *Rhododendron catawbiense* in existence. The species was discovered on Roan Mountain near the end of the eighteenth century by Fraser, who at that time was working for the Russian government (Gray, 1842). The presence of this profusely flowering shrub is perhaps the principal reason why Redfield (1879) wrote the following: "Dr. Gray has well said that it is the most beautiful mountain east of the Rockies."

ALDER BALD COMMUNITY

The alder bald community extends along the summit of Roan Mountain for a distance of about 5 miles, interrupted at intervals by stretches of mountain meadow. It is much less extensive westward, occurring in disconnected patches where soil moisture seems to be above average. Although alder is distributed throughout the bald area, it occurs in pure stands only to the east of Carvers Gap.

Location of Stands.

Since the best development of the alder bald community appeared in the region of Jane Bald, 4 of the 5 stands were located in this vicinity: Stand A on the northeast slope of Jane Bald at 5,800 feet; Stand B immediately eastward on a northwest slope of Elkhorn Bald at 5,800 feet; Stand C on the south slope of Grassy Bald Ridge at 5,900 feet; Stand D on the southwest slope of Grassy Bald Ridge at 5,800 feet; and Stand E on the southwestern exposure of Round Bald at 5,750 feet. The degree of slope for these stands varied from about 8 degrees in Stand A to about 15 degrees in Stands D and E.

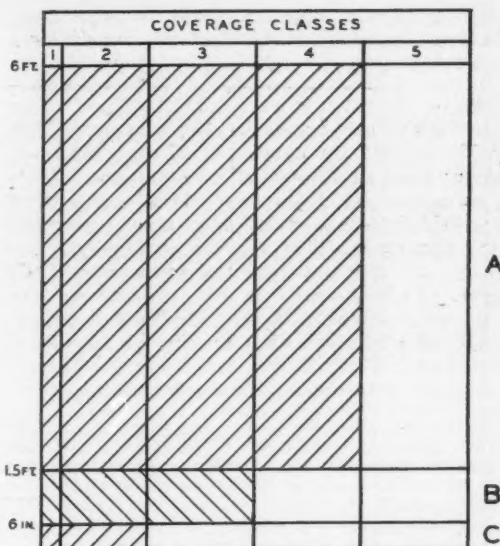


FIG. 20. Cover-stratification diagram for alder bald community.

- A. Shrub layer of *Alnus alnobetula* in pure stand.
 B. Herb layer of *Carex*, *Danthonia*, and *Rumex*.
 C. Moss layer of *Polytrichum*.

Wind velocity ranges from medium to strong, being strongest in Stand A and lightest in Stand D. Certain areas in Stand D were characterized by a high soil moisture as indicated by the presence of *Sphagnum* sp. which was not present in any other stands of the area.⁶ The largest and tallest clumps of *Alnus* occurred in this stand.

Stratification.

This shrub or "thicket" community is characterized by three layers: (1) a shrub layer, reaching a maximum height of 6 feet; (2) an herb layer, 0.5 to 1.5 feet high; and (3) a ground or moss layer, less than 6 inches high (Fig. 20). Only one tree species was recorded from the 100 quadrats, it being a *Sorbus americana* seedling 6 inches high; however, 3 more were seen outside the quadrats, a *Picea rubra* 6 feet high in Stand B and 2 *Sorbus americana* about 10 feet high in Stand D.

SHRUB LAYER

Frequency.

The floristic list for the alder bald community is presented in Table 18 with frequency and coverage data for each species. Since *Alnus alnobetula* was present in every quadrat analyzed except one in Stand E, its frequency is 99 percent. *Ribes rotundifolium* occurred only once in each of the 3 stands, showing a community frequency of 3 percent. The other woody species, *Menziesia pilosa*, *Rhododendron catawbiense*, and *Smilax glauca* occurred only in Stand A, each being present in only one quadrat. The stand frequency for each is 5 percent while the community

⁶ *Sphagnum* does occur, however, in wet places in the immediate vicinity of the Wilder Spring at 6,100 feet.

frequency is only 1 percent. Thus the shrub layer has only one species, *Alnus alnobetula*, which shows high frequency.

Density.

In Table 19 note that of the 149 plants present, 143 or 95.9 percent are *Alnus*, and of the 2,305 canes present, 2,288 or 99.3 percent are *Alnus* canes. There is an average of 16 canes per clump. These canes vary in height from 6 inches to 8 feet, averaging approximately 3.5 feet for the community. The clumps are uniformly spaced at an average of 1.3 meters (4.4 feet) apart. In areas of better development where clumps are taller and more dense, it becomes difficult to force one's way through this thicket community. *Rhododendron* ranks second with only two plants present on the 200 square meters surveyed.

TABLE 18. Frequency and coverage data for species of the alder bald community. Where two numbers occur opposite a species, the upper number represents frequency percent and the lower number represents coverage class. (August, 1936.)

Floristic list	Frequency percent and coverage						Distribution of coverage classes for the community					
Stand:	A	B	C	D	E	Community						
No. of samples:	20	20	20	20	20	100						
Altitude:	5,800	5,800	5,900	5,800	5,750							
Exposure:	NE	NW	S	SW	SW							
Slope:	8°	10°	12°	15°	15°		0	1	2	3	4	5
Woody species ¹												
<i>Alnus alnobetula</i>	100	100	100	100	100	100	2	3	26	44	24	
	3	4	4	4	4	4						
<i>Menziesia pilosa</i>	5					1		1				
	0					0						
<i>Rhododendron catawbiense</i>	5					1		1				
	0					0						
<i>Ribes rotundifolium</i>	5			5	5	3		2				
	0			0	0	0						
<i>Smilax glauca</i>	5					1		1				
	0					0						
<i>Sorbus americana</i>	5					1		1				
	0					0						
Pteridophytes												
<i>Dryopteris dilatata</i>	75	50	75	45	20	53	39	13	5			
	0	0	0	0	0	0						
<i>Polypodium virginianum</i>	20					4	3	1				
	0					0						
Herbs												
<i>Agrostis hyemalis</i>	45	45	40	80	80	58	53	4	1			
	0	0	0	0	0	0						
<i>Arisaema triphyllum</i>				5		1	1					
				0		0						
<i>Aster acuminatus</i>		5	10			3	2	1				
		0	0			0						
<i>Aster divaricatus</i>	5					1	1					
	0					0						
<i>Carex aestivalis</i>				15		3	1	1	1			
				0		0						
<i>Carex flexuosa</i>	5	20	30	65		23	6	15	2			
	0	0	0	0		0						
<i>Carex glaucoidea</i>				5	5	2	2					
				0	0	0						
<i>Carex intumescens</i>		10	15	50		15	9	4	2			
		0	0	0		0						
<i>Carex lucorum</i>	90	65	85	65	95	80	13	15	15	19	16	2
	3	2	3	2	2	2						
<i>Danthonia compressa</i>	5	40	75	85	60	53	19	19	8	5	2	
	0	1	2	1	1	1						
<i>Erechtites hieracifolia</i>			5			1	1					
			0			0						

TABLE 18 (Continued)

Floristic list	Frequency percent and coverage						Distribution of coverage classes for the community					
Stand:.....	A	B	C	D	E	Com-						
No. of samples:.....	20	20	20	20	20	muni-						
Altitude:.....	5,800	5,800	5,900	5,800	5,750	ty						
Exposure:.....	NE	NW	S	SW	SW	100						
Slope:.....	8°	10°	12°	15°	15°		0	1	2	3	4	5
<i>Heuchera villosa</i>			5			1	1					
			0			0						
<i>Houstonia serpyllifolia</i>	50	25	40	65	20	40	35	5				
	0	0	0	0	0	0						
<i>Isopyrum biternatum</i>						5	1	1				
						0						
<i>Juncoides echinatum</i>			5	25	5	7	1	3	1			
			0	0	0	0						
<i>Juncus effusus</i>				15	10	5	1	3	1			
				0	0	0						
<i>Juncus tenuis</i>				15	15	5	6					
				0	0	0						
<i>Lilium philadelphicum</i>				5		1	1					
				0		0						
<i>Maianthemum canadense</i>			5			1	1					
			0			0						
<i>Polygonum hydropiperoides</i>				5		1	1					
				0		0						
<i>Potentilla canadensis</i>				5		1	1					
				0		0						
<i>Potentilla monopetensis</i>					5	1	1					
					0	0						
<i>Rumex acetosella</i>	95	95	95	85	75	89	52	27	8	2		
	1	1	0	0	0	1						
<i>Saxifraga leucanthemifolia</i>	10	10		5	20	9	8	1				
	0	0		0	0	0						
<i>Trautvetteria carolinensis</i>	25					5	4		1			
	0					0						
<i>Trifolium saxicola</i>					5	1	1					
					0	0						
<i>Veratrum viride</i>	5		10	10		1	1					
	0		0	0		0						
<i>Veronica officinalis</i>				5		1	1					
				0		0						
<i>Viola blanda</i>	80	90	95	100	90	91	81	9	1			
Miscellaneous												
Moss and lichen cover ²	70	90	80	70	95	81	18	15	18	17	9	4

¹Seedlings included.

²*Sphagnum* sp. was present in 3 quadrats in Stand D, coverage 2 in each quadrat.

A few *Rhododendron* clumps were seen outside the quadrats within the area of the stands, and, since all appeared to be in a most vigorous condition, their presence brings up the question of dynamic trends which will be treated later.

Coverage.

There is only one dominant in the shrub layer, *Alnus alnobetula*, which covers about 65 percent of the total area (class 4). Rarely do *Alnus* clumps produce a closed canopy. There are numerous small openings which constitute about one third of the total area.

HERB LAYER

Frequency.

Only two species of the herb layer belong to Frequency Class E, *Viola blanda*, 91 percent frequency, and *Rumex acetosella*, 89 percent frequency. There is only one species in Class D, *Carex lucorum*, fre-

TABLE 19. Density by height classes of woody species present in the alder bald community. (Based on 100 quadrats 1 by 2 meters.)

Species	Clumps (plants)	Canes per clump	Height in feet: number of canes								Total canes
			0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	
<i>Alnus alnobetula</i> ..	143	16	7	174	784	893	265	140	...	9	2,288
<i>Rhododendron catawbiense</i> .	2	3	4	7
<i>Menziesia pilosa</i>	1	..	1	4	5
<i>Ribes rotundifolium</i>	1	1	2	3
<i>Smilax glauca</i>	1	1	1
<i>Sorbus americana</i> seedlings.....	1	1	1
Totals.....	149	16	8	182	789	896	265	140	...	9	2,305

quency 80 percent. Three species belong to Class C: *Agrostis hyemalis*, 58 percent; *Danthonia compressa*, 53 percent; and *Dryopteris dilatata*, 53 percent. Class B is represented by two species, *Houstonia serpyllifolia*, 40 percent, and *Carex flexuosa*, 23 percent. Of the 23 species in Class A, *Carex intumescens* ranks first with a frequency of 15 percent, followed by *Saxifraga leucanthemifolia*, 9 percent; *Juncoides echinatum*, 7 percent, and *Juncus tenuis*, 6 percent. Each of the remaining 18 species shows 5 percent frequency or less.

Species of the herb layer present in all 5 stands are: *Carex lucorum*, *Dryopteris dilatata*, *Agrostis hyemalis*, *Danthonia compressa*, *Houstonia serpyllifolia*, *Rumex acetosella*, and *Viola blanda*. *Carex flexuosa* and *Saxifraga leucanthemifolia* were present in 4 stands. Of the remaining 22 species, only 8 occurred in more than one stand. Thus it is seen that about one fourth of the species of the herb layer are widely distributed throughout the community while the remaining species tend to be present locally only. Of these widely distributed species, *Viola blanda*, *Rumex acetosella*, and *Carex lucorum* are most frequent, while such species as *Carex aestivalis*, *Aster acuminatus*, *Juncus effusus*, and *J. tenuis* best represent locally established species.

Coverage.

The 3 species which cover more than 1 percent of the surface sampled are: *Carex lucorum*, class 2; *Danthonia compressa*, class 1; and *Rumex acetosella*, class 1. The combined coverage of all the other species of this layer is less than 5 percent of the total surface. Thus *Carex lucorum* is dominant in the herb layer with *Danthonia compressa* and *Rumex acetosella* as sub-dominants. All species of the herb layer cover about one half of total surface and show their best development in the open areas between alder clumps.

GROUND LAYER

Mosses and lichens occurred in every stand with an average frequency of 81 percent for the community,

ranging from 70 to 90 percent in each of the stands. *Polytrichum commune* is the dominant ground species. There is a uniform distribution of the moss and lichen cover throughout the community as indicated by its high frequency. Degree of cover varies from less than 1 percent in some quadrats to more than 75 percent in others as shown by its distribution in all the coverage classes (Table 18) while the average coverage for the community is approximately 15 percent (class 2). *Sphagnum* sp. was present in 3 quadrats in Stand D and covered about 15 percent of the area of each quadrat.

COMMUNITY AS A WHOLE

This shrub community is dominated by only one species, *Alnus alnobetula*, a species with a limited distribution in this country, probably showing its best development on Roan Mountain. This shrub grows in almost pure stands 3 to 4 feet high and covers about 65 percent of the total surface (Fig. 23). In a few places the coverage is almost complete, but throughout the greater extent of the community small openings of 2 or 3 square meters between clumps are common. These openings are usually dominated by *Carex flexuosa*, *Danthonia compressa*, and *Rumex acetosella*, *Carex flexuosa* being most important. The moss layer covers less than one fourth of the surface and is dominated by *Polytrichum commune*.

SUCCESION

BEECH-MAPLE COMMUNITY

The beech-maple community is climax for the altitudinal zone (3,500-5,000 feet) in which it occurs. In general, as indicated by reproduction and survival of dominants, the community appears to be maintaining itself within the deciduous zone. In the extreme upper limits of this zone, yellow birch is dominant and in places gives way to conifers. A good example of such invasion is in Carvers Gap where there are several large relic birches, some of which are dead. Hataya (1933) found a similar condition to be true on Mt. Fuji and says that its birch forest is being replaced by conifers.

SPRUCE-FIR COMMUNITY

The spruce-fir forest is climax at the higher altitudes (5,500 feet to the summit). There is no sign of natural decadence of this community within the area under study, but there is most convincing evidence that it is a vigorous, aggressive community. This is supported by statistical data recorded in the phytographs (Fig. 13) which show that the important trees are represented in the five different size classes. No area was found in which conifers were giving way to any other species.

Secondary succession in the spruce-fir community was determined by repeated observations made each summer within the cut-over areas. All stages were observed from immediate cutting to those nine years old, and in a few instances to some half a century old. These observations were supplemented by statistical data recorded from 25 quadrats 2 by 2

meters located at the head of a cove on the southwestern slope immediately below Wilder Spring. In this area, which in general is representative of the higher cut-over conifer lands, sedges, especially *Carex flexuosa*, became established rapidly and soon covered 10 to 15 percent of the ground surface. *Rumex acetosella* soon appeared with a cover as great as the sedges. The first shrubs were mountain blackberry (*Rubus canadensis*) and red berried elder (*Sambucus racemosa*) with a cover of 10 to 25 percent. Pin cherry (*Prunus pennsylvanica*) was usually associated with these shrubs in varying proportions but was less important in the area sampled than in most cut-over areas on the mountain. The thicket stage was replaced by conifers which became established in the shade. They finally push through the thicket canopy and become the climax dominants. In some places conifers appear directly without the usual intermediate herb and shrub stages.

Korstian (1937) describes in detail secondary succession for the spruce lands of the Southern Appalachians. Some of the data were taken from Unaka Mountain, Unicoi, Tennessee, which is within twenty-five miles of Roan Mountain. His studies show that yellow birch (*Betula lutea*) and shrubs for a time often dominate an area from which conifers have been removed by logging. This is in accord with conditions in the lower portion of the cut-over conifer zone of Roan Mountain.

BALDS

Careful observations have been made throughout the full extent of the balds to determine successional trends. Along ecotones, a number of detailed statistical samples were taken, including 5 belt transects, 3 sets of "intermittent strip samples," and 3 permanent chart quadrats. In addition, a total of 100 quadrats was tallied in four widely different situations of the grassy bald community. In this discussion, it seems desirable to present only the significant results of these studies, supplemented by certain diagrams and photographs. Tension lines between communities are definitely changing. This shifting of tension lines between any two communities is always in the same direction and signifies that succession is now taking place at such points.

GRASSY BALD COMMUNITY

The grassy bald is being invaded by rhododendron, conifers, and alder. The best examples of invasion



Fig. 21. Invasion of grassy bald by conifers. Conifers in background have invaded the area they now occupy within the past half century. Immediately west of Carvers Gap, looking westward. Altitude, 5,500 feet. August, 1937.

of the grassy bald by rhododendron are found along the summit west of Roan High Knob. Good examples of grassy bald invasion by conifers are found along the margin of the balds from 5,500 to 6,200 feet altitude (Figs. 21 and 25). Invasion of these balds by alder is less conspicuous and is best seen on the eastern end of Grassy Bald Ridge.

INVASION BY RHODODENDRON

By mass invasion rhododendron (*Rhododendron catawbiense*) appears to be replacing the grassy bald community. An example of such invasion is to be found along the southern margin of the grassy bald immediately southwest of Roan High Knob (Fig. 24). A belt transect study (2 by 100 meters) made in this area shows an abundant supply of rhododendron seedlings, even as many as 20 per square meter in some areas. The greatest density occurs in partial shade of older clumps, but it was not uncommon to find seedlings in an open grassy bald several meters from a rhododendron clump. Seeds either germinate directly in the grass or in moss clumps, there being a slightly higher percentage of germination in moss clumps. Survival of seedlings seems to be high, since very few dead ones were observed in the transect or elsewhere within the grassy bald. That this invasion is positive and of a permanent nature is evidenced by a vigorous representation of rhododendron across the ecotone, ranging from seedlings in the open area, to plants 75 years of age within the rhododendron bald community. It is most unusual to see a dead clump of rhododendron anywhere in the treeless area.

Detailed observation of other areas reveals the same general condition described above. More rapid invasion is usually along depressions while slower invasion is along the more elevated portions of the grassy bald, a condition which might be explained by an adequate soil moisture study. The rate of invasion, since it varied for each particular location, was not determined; but it is safe to say that, in some places, rhododendron advances into the grassy bald as much as a meter a year.

INVASION BY CONIFERS

In certain areas, as along the ecotone between the grassy bald community and the spruce-fir forest, conifers (*Abies Fraseri* and *Picea rubra*) invade the grassy bald directly. Such invasion is more rapid along the northern margin of the grassy balds than elsewhere on the mountain. A splendid example of this condition may be seen on the northeast slope of the ridge immediately west of Carvers Gap (Fig. 21). A transect (2 by 114 meters) was run across the ecotone at this station and the general condition is shown in Figure 25. Seedling conifers usually establish themselves in small moss clumps or by the edge of rocks, but they very often become established directly in the grass. An examination of seedlings that survive in grass showed that some moss was usually present where they became established. The statistical study of the grassy balds shows that moss plants occur throughout the whole area and, when

not in "hummocks," are closely associated with grass culms.

Between the edge of the grassy bald and the advancing coniferous forest there is often a zone of moss (*Polytrichum commune*) 1 to 5 meters wide appearing as a solid "moss carpet" 6 to 12 inches deep (Fig. 26). Such growth also occurs in certain openings just back of the forest margin. The mountain oat grass (*Danthonia compressa*) does not thrive in this dense carpet of moss as evidenced by many dead bunches found within it. The moss carpet advances slightly ahead of the coniferous forest, maintaining about the same width as it encroaches upon the grassy bald. Its appearance may be due to the rapid growth and development of moss plants which, previously suppressed in the slightly xeric grassy bald, become dominant when a more mesic condition occurs. Since such a moss carpet does not occur except in areas within a few feet of conifers, it appears that the forest is either producing a more mesic condition or that it is invading areas becoming more mesic due to other causes. As Toumey and Korstian (1937) have shown, site affects vegetation, and vegetation affects site which in turn is reflected in vegetation. This reaction concept helps explain the above situation.

The conifers produce a more mesic condition by shading and reducing wind velocity. The moss carpet then develops and affords a better condition for the germination of seedlings than exists in grass. Observations revealed that coniferous seedlings become freely established in this moss carpet and show high survival value. Seeds which had lodged between moss plants germinated far more readily than those which lodged between grass culms. Upon germination, the radicle grows downward rapidly between the moss plants to regions of greater moisture. Examination of seedlings 2 to 5 years of age revealed that in most cases the tap root turns at a depth of 3 to 6 inches and grows in a horizontal position. When the conifer canopy shades the area, the moss is suppressed and the heavy carpet disappears.

The effect of trampling is indicated in certain areas grazed by cattle and sheep where many small coniferous seedlings die. The numerous dead seedlings examined revealed a scar at ground level such as might be made by the hoof of an animal.

Examination of spruce and fir trees growing in the grassy bald and within the spruce-fir forest showed a sharp contrast between growth forms. Trees growing in the open develop pyramidal crowns extending to the ground and short, knotty, tapering boles with branches throughout their length (Fig. 28A), while trees growing under forest canopy develop short terminal crowns and clear boles 20 to 60 feet in length (Fig. 28C). In the upper portion of the coniferous forest area, several trees of the former type were found among a forest of the latter type. Since such trees were too knotty to have been split for pulp wood, they were left in the cut-over area, and are now conspicuous objects on the landscape, standing alone as they once did in a one-time treeless area (Fig. 34). Some of them are located as far as 100

meters back of the forest margin. Evidently such trees became established in the grassy bald directly. One finds very few dead coniferous logs near the upper limit of the forest zone as compared to lower portions of this zone, indicating that the upper marginal portion of the forest is little if any older than the oldest trees now within it. Many coniferous stumps with 300 to 350 annual rings occur near the middle of the spruce-fir zone while very few stumps with more than 150 annual rings occur within 50 meters of its upper margin. Upon this basis, an area of more than 100 acres now supports a forest which is apparently less than a century old. Thus the spruce-fir forest of Roan Mountain is relatively young, especially along the upper and eastern limits, and has not reached a maximum development in more than half of the area occupied by it. Neither has it yet covered its total potential area as evidenced by its present advance into the balds.

A 72-year-old native of the southern slope of Roan Mountain, Cane Freeman, remembers the time when a spring, located on the north slope about 100 meters within the forest, was at the margin of what was then a grassy bald along this ridge. The present-day vegetation supports his statement. Evidently the balds were once more extensive than they are now and, from present indications, they are and have been slowly giving way to northern coniferous forest.

INVASION BY ALDER

In a few places along Roan Mountain, as in the vicinity of Jane Bald (Fig. 22), a vigorous growth



FIG. 22. Looking east from the east slope of Round Bald towards Grassy Ridge Bald. The alder bald community has its best development near the crest of the ridge which appears at the horizon. The first rounded peak (center) is Jane Bald. Note the physiognomy of the grassy bald community in the foreground. A small island of conifers appears at the southeastern end (right) of Grassy Ridge Bald. September, 1937.

of alder (*Alnus alnobetula*) appears to be slowly encroaching upon the grassy bald. Cane Freeman, previously cited, says there is more alder in this vicinity than when he was a boy. Jane Bald was so named because an old gray mare, once owned by a woman named Jane, preferred to graze on this spot. At present this area is not suitable for grazing.

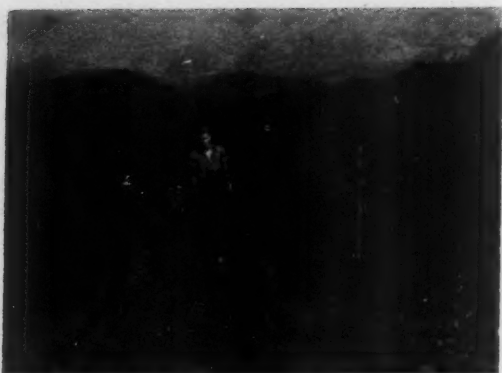


FIG. 23. A good development of the alder bald as it appears on the extreme western end of Grassy Ridge Bald. Mountain alder (*Alnus alnobetula*) rarely occurs this densely on Roan Mountain and appears to be uncommon elsewhere. August, 1937.

RHODODENDRON BALD COMMUNITY

Rhododendron occurs in almost pure stands on the western summit of the mountain. The quadrat data (Table 6) reveal that conifer seedlings frequently occur under the shade of rhododendron, and that in places they break through the shrub canopy and survive.

There are abundant examples of such invasion of the rhododendron bald. Figure 24 shows a condition



FIG. 24. Diagram showing double invasion. Rhododendron invades the grassy bald and conifers invade the rhododendron bald. R, Rhododendron; A, Abies; P, Picea. The dots represent rhododendron seedlings and the shaded pyramids represent coniferous seedlings. (Based on a transect, 2 by 100 meters located immediately southwest of Roan High Knob.)

existing immediately southwest of Roan High Knob which is typical of rhododendron balds of the area under study. Coniferous seedlings become established both in the open and under the shade of rhododendron plants. The number of conifers that germinate and survive in the rhododendron bald seems to depend primarily upon two factors, the amount of soil moisture and a suitable seed supply. Good survival is



FIG. 25. Diagram showing invasion of the grassy bald by conifers. A, Abies; P, Picea. The shaded pyramids represent conifer seedlings under 1 foot high. *Betula* seedlings under 1 foot high are represented by the small open circles.

evidenced by the presence of seedlings and trees of different sizes and ages. Conifers frequently become established in scattered rhododendron clumps where they soon overtop the clump and eventually "choke" it out. These conifers often serve as parent trees for another wave of invasion, either directly into the grassy bald area (Fig. 29) or into other rhododendron clumps.

Additional evidence explaining the dynamics of this community was obtained by making a comparative study of the growth forms of rhododendron plants present in shade and in the open. Many different stages of invasion were studied, ranging from establishment of seedlings under rhododendron to elimination of rhododendron by a dense canopy of conifers.



FIG. 26. View of moss carpet which is being invaded by conifers. Immediately west of Carvers Gap. August, 1937.

Rhododendron plants growing in the open become hemispherical in shape, much resembling shocks of hay or wheat (Figs. 20 and 27A). This is obviously an adaptation which permits a maximum exposure of leaf surface with a minimum rate of transpiration. The height of a plant growing in the open rarely exceeds 4 feet, which is usually less than the diameter of its crown. As the clumps within an area become more closely spaced, following invasion, the height increases with a corresponding decrease in diameter. Since light is now received chiefly from above, the clumps assume an ob-conical or corymbose shape (Fig. 27B), a condition typical of clumps in better developed areas of the rhododendron bald community. The maximum height of clumps observed in such areas was 9 feet. By this time invading conifers have pushed through the canopy in certain more favorable places (Fig. 27C). The rhododendron canes under dense shade of conifers begin to die while the canes in partial shade grow rapidly in length, resulting in plants less branched and more slender than those of the open area (Figs. 27D and 27E). Before this time the rhododendron under which the first conifer became established has long since been dead, but its canes, not yet decayed, definitely show that its growth form was determined in the open. Other clumps not so close to the first co-

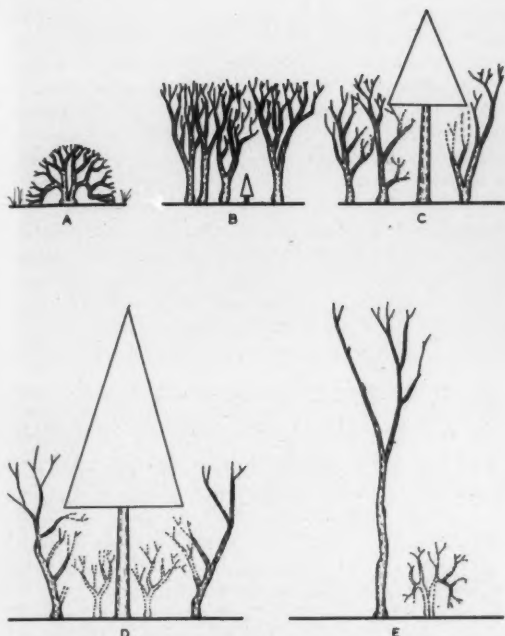


FIG. 27. Diagrams showing successive changes in growth form of *Rhododendron catawbiense* as it becomes invaded by conifers.

- A. Conical shape of plants growing in open.
- B. Corymbose shape assumed by plants in a normal stand of rhododendron. Conifers establish themselves under the shrub canopy.
- C. Heavily shaded branches die (dotted lines) while lightly shaded ones lengthen.
- D. Two dead plants which once grew without shading from above and two other plants in which all recent growth has been toward light with dying of heavily shaded branches.
- E. Typical rhododendron plant as it occurs under forest canopy.

nifers that invaded, survive by an adaptation in which the plant branches less than in the open and grows very tall, often exceeding 12 feet in height. Finally these are eliminated by the increased crown density of the invading forest (Fig. 30).



FIG. 28. Diagrams showing growth forms of conifers as determined by light. A, growing in the open with light from above and all sides to the ground level. B, growing in shrub bald with light from above and sides to within 6 to 10 feet of ground. C, growing within the spruce-fir forest with light principally from above.



FIG. 29. A late stage of invasion by conifers in which rhododendron has been almost completely smothered out. Note numerous seedlings which have established themselves in the grassy bald near the parent tree. August, 1937.

An excellent example of invasion of rhododendron bald on a large scale is to be found at the southwestern limit of what is now known as the rhododendron garden. The forest along the western border of this area has recently replaced 25 to 50 acres of rhododendron and is still advancing, not only from the west, but also from the north and the south (Fig. 30). Most of the trees of this forest area have short, tapering and knotty boles with but few branches below 6 feet (Figs. 28B and 33), showing that they became established under rhododendron. Ring counts show the average age to be less than 40 years and the maximum age less than 65 years.

The growth forms of rhododendron plants and coniferous trees, the presence of large, dead rhododendron stems, the absence of dead tree trunks, and the abundance of coniferous reproduction provide striking evidence of the youthful and aggressive condition of that portion of the spruce-fir forest described above.

From the foregoing it becomes clear that the rhododendron bald community in the area under study is sub-climax, giving way to the spruce-fir climax forest community.

ALDER BALD COMMUNITY

Successional trends are less conspicuous in the alder bald community than in the other bald communities of the area but alder is invading in some places and is being invaded in others. In areas of better development, as on the northwest slope immediately east of Jane Bald (Fig. 23), the growth of alder is quite vigorous and is apparently maintaining itself. In areas of weaker development, as along the western and extreme eastern limits, alder appears to give way to rhododendron and conifers.

Two sites were observed where rhododendron appears to be invading the alder. The first example is within a small sedge bald about one fourth of a mile west of Carvers Gap along the main divide. Here alder and rhododendron were found growing with canes intertwined. Ring counts of a number of canes

of each species showed that alder invaded the area many years ahead of rhododendron. The other site is on the southwest end of Grassy Bald Ridge where several dozen small, vigorous clumps of rhododendron were present. By counting 50 clumps of alder at random, it was found that 12 of them were dead. No dead clumps of rhododendron were observed here. Thus, it seems that rhododendron succeeds where alder fails. This condition is typical of many acres on this end of the mountain. The cause is unknown, but since fire has occurred within the balds, it has probably been the chief factor in elimination of alder. Damage to alder has also been caused by defoliating insects. Rhododendron seems to be more tolerant of fire and insects than alder.

Based on data from 37 quadrats 2 by 2 meters which were taken along a line extending from Roan High Knob northeastward to the margin of the coniferous forest, rhododendron appears three times as important as alder, the two species forming a very dense and tangled thicket. A comparison of the two species as to ring counts, dead wood, reproduction, relative tolerance under conifers, and sociological dominance, shows that alder is slowly giving way



FIG. 30. Young spruce-fir forest which has recently invaded and replaced what was once a rhododendron bald. Many trees had reached sufficient size to have been cut for pulpwood. This area extends to Roan High Bluff and contains more than 50 acres. From southwest end of rhododendron garden, looking southwest. May, 1938.

to rhododendron. Harshberger (1903) in describing the vegetation of the summit of Roan (evidently the area described above) says, "*Alnus alnobetula* clings to the north slopes, here forming a pure growth on the steeper inclines (*Alnus* Association), with *Sorbus americana* below it, but associated with *Rhododendron catawbiense* on the upper slopes of the dome." At present there is no pure growth of alder in this vicinity, but as just revealed there is more rhododendron than alder. Evidently there has been a definite change in the floristic composition of this particular area immediately north of Roan High Knob within the past 35 years.

The presence of conifers (Fig. 31) which show high survival value, indicates that at this station alder will eventually give way to the coniferous forest climax.



FIG. 31. Looking west from Roan High Knob. Invasion of the mixed alder-rhododendron thicket community by conifers shown in foreground. August, 1937.

A few advanced stages of invasion of alder by conifers were observed on the extreme eastern end of Grassy Bald Ridge where conifers have formed a young closed stand. Thus, alder appears to be sub-climax and may be replaced by conifers directly or by rhododendron and then by conifers.

HISTORICAL VIEWS BEARING UPON BALD SUCCESSION

Mitchell (1835) perhaps first mentioned the treeless condition on the summit of Roan Mountain. He wrote, "With the exception of a body of rocks looking like the ruins of an old castle, near the southwestern extremity, the top of Roan may be described as a vast meadow, without a tree to obstruct the prospect; where a person may gallop his horse for a mile or two, with Carolina at his feet on one side and Tennessee on the other." This statement appears significant since it emphasizes the existence, at that time, of large stretches of grassy bald. Evidently this author was describing the area extending from Roan High Knob to Roan High Bluff, all of which now supports too many shrubs and trees to allow one to gallop a horse for more than a quarter of a mile in any direction.

Gray (1842), in a letter to Sir William Hooker, described a collecting trip to Roan Mountain in 1841 and quoted Mitchell's description given above. This indicates that Gray was also impressed by the great expanse of mountain meadow. In describing his collecting on the rounded bald of the southwestern summit, he says, "The only tree is *Abies Fraseri*, a few dwarfed specimens of which extend into the open ground of the summit." He did not commit himself as to the origin or trends; but apparently what he then described as a grassy bald being invaded by *Abies Fraseri* is now a forested area (Fig. 30).

Redfield (1879), in describing the last trip of Asa Gray and party to Roan Mountain, mentioned the balds of the mountain. He says, "Much of the summit prairie flora has been doubtless destroyed by the large herds of cattle, horses, and sheep, which every summer are sent to the mountain for pasture." This



FIG. 32. Growth forms of rhododendron plants as found under spruce-fir canopy. Knots at base of the clump near the center indicate that this plant became established and lived for some time in an open area. Most of the dead twigs on the ground are those which dropped from the lower portion of this clump and other similar clumps. The tall slender dead canes of this clump show that they developed in shade after the area became invaded by conifers. May, 1938.

statement indicates that he considered the native species of the grassy balds to have once been more important than at the time of his visit. Another statement of his in which he says, "There is some reason to believe that the forest of spruce-fir has been encroaching upon the bald portion of the summit, but as it is now being cut for firewood and fencing, any such encroachment is likely to be checked, perhaps too effectually," shows that he believed the area was passing from a "mountain meadow" to a spruce-fir climax.

Harshberger (1903) described the balds of Roan Mountain as a "sub-alpine treeless formation" and made the first attempt to explain the cause of the balds by saying that they were the result of ice-storm injury. He assumed that frozen twigs were snapped off and trees thus eliminated to be replaced by vegetation of another type. His conclusion was based principally upon Edson's study (1894) in which she described frost forms on Roan Mountain. She did not, however, discuss the effect of snow and ice on trees or suggest the cause of the balds.

Davis (1930) considers the grassy balds of the

Mount Mitchell region as of natural origin. He says there is no legend of Indian occupancy or of fire. Relative to the heath balds he states: "These heath balds seem to be encroaching upon the grassy balds but there is no indication of the development toward a forest type. Neither fire nor cut-over seems to explain their origin. They are best considered as physiographic-edaphic climaxes."

Cain (1930), who made a statistical study of the heath balds of the Great Smokies, describes them as having been derived from forested types by the elimination of tree species and considers them as "post-climax 'islands' in the contiguous coniferous and broad-leaf formations." In describing the grassy balds in the following year (1931) he says, "... in all probability these balds are natural phenomena. . . . It is sufficient to mention that soil profiles show from a few inches to a foot or more of homogeneous black soil of grassland type, which is far too deep to have developed since the advent of the white man. . . ."

Camp (1931) says, "The grassy balds were originally meadows containing numerous clumps of low shrubs, predominantly ericaceous, with higher shrubs at the margin." He holds that the grassy balds of the southwestern portion of Gregory Bald, located in the Great Smokies, are natural phenomena, probably



FIG. 33. A parent spruce which evidently became established under shade of rhododendron as indicated by absence of branches lower than 5 feet. This tree is located at the present southern margin of grassy bald immediately west of Cloudland Lodge. May, 1938.



FIG. 34. A parent tree which probably became established in the grassy bald. This tree was far too knotty to have been used for pulp wood. May, 1938.

produced by occasional desiccating southwesterly winds. "In midsummer," he says, "there are occasional periods of excessive drought, and it is this extreme that limits the character of the bald rather than the general climatic mean."

Fink (1931) does not believe these balds to be of Indian origin because it would have been too great a task for the early Indians to have cleared the balds since they lacked both tools and energy.

The foregoing authors have either assumed a theory of natural origin of balds or else have suggested no explanation. Wells (1932, 1936, 1937) has recently proposed a theory of Indian origin to explain the presence of the grassy balds of the Southern Appalachians. Based on a study of 23 grassy balds, he concludes that these balds were initiated by human interference at soil level which destroyed forest vegetation and resulted in the development of grassy balds. His assumption is that this disturbance was due principally to tramping of Indian feet, perhaps supplemented by tramping of their horses and cutting of trees for firewood. He imagines that the Cherokees spent much time on the summits of our higher mountains, congregating there in large numbers during the warmer months for hunting, camping, or perhaps warfare. "A grass bald," he says, "is in a sense an expanded trail." Wells (1937)

describes the summit of Round Bald as having been the original Indian bald on Roan Mountain.

DISCUSSION

PROBABLE ORIGIN OF BALDS

These writers have suggested only three causal factors to explain the presence of the balds. Harshberger's ice-storm theory and Camp's theory of desiccating summer winds both suggest the factor of local climate. The "physiographic-edaphic" factor of Davis is a concept of the Cowles school.

The Indian theory of Wells is one of mechanical disturbance of the vegetation at soil level. This theory is not in accord with the facts revealed by the vegetation itself within the area under study. In the first place, the writer can find no evidence that Indians ever spent enough time on this mountain to have produced even slight changes in the vegetation. Artifacts have been searched for throughout the whole area, especially on the summit of Round Bald and in the vicinity of the two large springs at Carvers Gap, but nothing has yet been found. Inquiries have been made of older citizens, but none have heard of Indians having lived or camped on Roan Mountain. Judge S. C. Williams, historian for the State of Tennessee, and a resident of Johnson City, Tennessee, has devoted much time to study and writings concerning

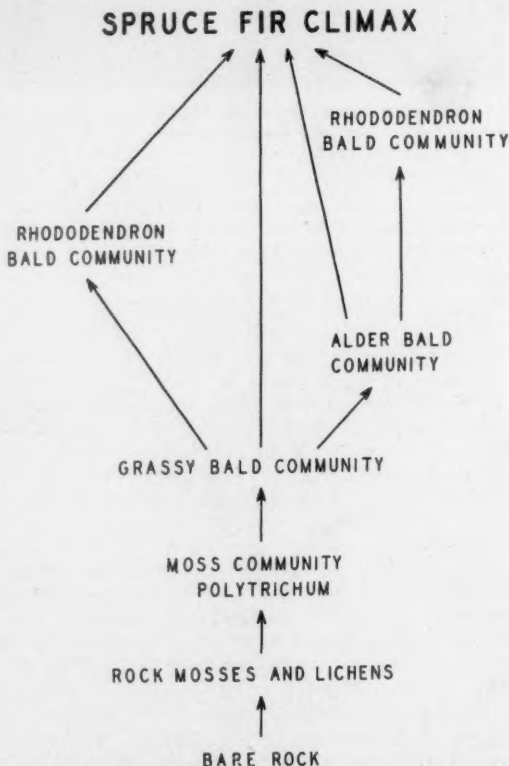


FIG. 35. Probable course of succession on the summit of Roan Mountain.

this East Tennessee country. Recently he said that it was not the custom of the Cherokees to frequent high mountains except to cross them in moving to a new location. He does not believe the Indians had anything to do with the origin of the balds and considers such an idea absurd.

The following excerpts from a letter received from M. W. Stirling, Chief, Bureau of American Ethnology, Smithsonian Institution, further discounts the theory of Indian origin of grassy balds: "... the historic sites of the Cherokee are southwest of Roan Mountain. At an earlier date they probably lived in the neighborhood, but we do not know what their customs may have been at this early time. . . . It seems unlikely that a mountain summit would be cleared for any purpose, unless under very exceptional conditions."

Even though one does assume that Indians camped along mountain summits, it would appear more logical that they did so because attracted by pre-existing balds rather than that their presence initiated the development of the balds. Even if Indians had made extensive trails, there is no evidence from this study that such trails would have become expanded into balds. On the other hand, there is abundant evidence that trails on Roan Mountain tend to close up rather than to expand. The present day sheep trails on Alder Bald are usually less than a foot wide and are worn down to a depth of more than 6 inches in places. Alder canes overlap the trail and after more than a century of use these trails, more than a mile in extent, have not expanded. Another old trail is the one leading from the southwestern end of the present rhododendron garden to Roan High Bluff. This trail has been used extensively by both man and beast for more than a century, and even though it leads through grass, shrub, and forest communities, there is no sign of expansion.

The locations of old horse and cattle trails, abandoned more than half a century ago, were determined within the present pure stand of rhododendron. This observation indicates that the trails were made within grassy areas which have since been replaced by rhododendron. Rather than trails producing grassy balds by their expansion, grassy balds may even contract and eliminate previous trails within their area by an invasion of shrubs or trees or both.

On the northeast slope of Round Bald there is a community of buckeye (*Aesculus octandra*) existing in an orchard condition. The growth forms of the trees indicate that they were not produced within a forest but rather in open areas. Since dead trees were frequent and reproduction weak, it appears that these trees are on the decline. Fire, grazing and browsing, and some cutting to improve grazing have been apparently responsible for this decline. No trees exist on the very summit of this bald. Perhaps windfall has been an important factor in the elimination of trees from this summit. Increased transpiration and decreased soil moisture of the heavily exposed dome-shaped summit may have been factors of greater significance.

An excellent example showing the effect of windfall in the elimination of trees and their subsequent replacement by grass, is a grassy bald area about 15 by 40 meters extending as a "peninsula" into the hardwoods of the southwest slope of Round Bald. Many old logs with long, straight boles are located in this grassy spot which is bordered by trees with clear boles 30 to 40 feet, showing that the area was once forested.

Another example of grassy bald having replaced hardwoods is at Carvers Gap where a forest "isthmus" once connected the hardwood forest area of the south slope with that of the north slope. Natives who have known the area for more than half a century told the writer that a cabin once stood in the gap and that hardwoods were cut to supply firewood for this cabin as well as for the hotel at Cloudland. Several small buckeye, hawthorne, beech and a few birch trees still stand as relics. A number of large, dead trees, evidently uprooted by wind, show the dangers of windthrow subsequent to opening this forest by cutting.

In both cases, the grassy bald has replaced the trees and appears to be maintaining itself. Whether or not hardwoods will eventually invade this area remains to be seen. There is no indication at any place along the ecotone between grassy bald and hardwoods that, under *natural conditions*, either community is giving way to the other, save the tornado case cited above.

SPRUCE-FIR ADVANCES BETWEEN GRASSLAND AND HARDWOOD

It appears significant that the spruce-fir forest has been slowly advancing eastward from an original center of distribution in the vicinity of the southwestern summit. Parallel invasions have occurred on the two slopes of the divide, north and south, in which the coniferous forest advances as a "wedge" along the ecotone between the grassy bald and the hardwoods. This forest spreads by mass invasion into the bald areas, there being very little advance into the hardwoods. A small "island" of conifers occurs on the southeastern end of Grassy Bald Ridge. Below, these conifers are bordered by hardwoods (birch, beech, and maple) and above, by alder and rhododendron which they invade. There are no conifers or rhododendrons within many miles of this area except on Roan Mountain to the west of Carvers Gap, a distance of 2 miles or more. Since migration of rhododendron and conifers is essentially by wind, and since the prevailing winds are from the north (sometimes from the south but rarely from the east or from the west), this "island" of conifers and rhododendron appears to be a new or secondary center of distribution for these species on that portion of Roan east of Jane Bald. It is probable that this "island" originated by rhododendron having become established in what was once a grassy or alder bald and which subsequently became invaded by conifers.

Griggs (1934), in a careful study of the timber line in Alaska, has shown that forest there has been continuously advancing northward into new territory. He

obtained most reliable evidence from the growth forms of old parent trees located some distance back from the forest edge. He explains that old trees with large branches all along the boles indicate that they developed in the open before a closed forest condition had yet been reached. The picture presented by the growth forms of rhododendron and conifers in the area under study, as previously described, is in accord with Griggs' findings.

IS OUR CLIMATE CHANGING?

The only adequate explanation of the dynamic trends in the vegetation on Roan Mountain seems to lie in the concept of climatic change. Unless it is agreed that for the first time in the vegetational history of this area, the grassy balds have come to the end of their long sustained sub-climax stage and are gradually giving way to a forest, the first to occupy the area in question, it must be assumed that climate has changed recently or is now changing, and that such changes are being reflected in the vegetation.

May not climatic change and plant migration be in progress at the present time? The common generalization that any factor which has operated throughout the vast ages of the past has had sufficient time to have long since produced stabilization, needs rethinking. Griggs (1937) has pointed out that vast changes, due to changes in climate, have taken place within the past 1,000 years or so. Among them he cites the following examples: (1) Syria is becoming too arid for agriculture; (2) the old Norse colonies in Greenland which once thrived on dairying, now lie buried in the ground perpetually frozen; and (3) plant migrations are now in progress as in the past. He also concludes that the recent advance of forest in Alaska is due to climatic change.

As a result of this phase of the study dealing with succession, it appears to the writer that insufficient soil moisture, at times critical to woody seedlings, best explains the long period during which the balds have apparently maintained themselves as a sub-climax. As Cox (1933) has stated, it is not the average but the extreme conditions which happen only occasionally that are most important in determining vegetational changes. The mild drought of June, 1936, was responsible for the death of some conifers that had become established in the grassy bald in the vicinity of Carvers Gap. Should such a condition recur only once every few years, invasion of the grassy bald by coniferous forest would be retarded or perhaps stopped completely. Thus, it appears that the present and recent advance of shrubs and conifers into the grassy area has been due primarily to a shortening of dry periods at critical times. The precipitation mean need not have changed since there is an abundance of rainfall within the area if properly distributed as to time. The balance between precipitation and vegetational change at extremely critical times is most delicate, even so sensitive that the appearance of a shower or even a cloudy or foggy day just before the crucial period is reached, may result in the survival of seedlings which otherwise

would have perished. The factor of grazing, and subsequent occasional fires set to improve grazing, have served merely to check normal trends in succession rather than to have caused them. Such factors tend to maintain the grassy balds for a slightly longer period than would have been expected under natural conditions.

The problem of "bald origin" is not yet solved, but it is felt that this study represents a closer approach to the true explanation than has appeared hitherto. Before a solution is finally reached, further study of certain edaphic factors, particularly soil moisture, seems advisable.

SUMMARY

1. A statistical study was made of the plant communities of Roan Mountain during the growing seasons of 1934, 1936, and 1937.

2. The area under study is the major portion of Roan Mountain, altitude 6,285 feet, located along the northern portion of the Tennessee-North Carolina state line. As compared to the surrounding country, the climate of this area is characterized by lower temperatures, higher precipitation, higher wind velocities, less sunshine, and a shorter growing season.

3. The vegetation is considered to belong to either a forest or grassland type. Altitudinal zonations of the forest communities are: (1) beech-maple, 3,500 to 5,500 feet; and (2) spruce-fir, above 5,500 feet. Grassland communities (including shrub balds) occur from 5,500 feet to the summit.

4. The beech-maple community is composed of a superior tree layer consisting of beech, maple, and birch with some buckeye and service berry; an inferior tree layer of mountain maple and striped maple; a shrub layer dominated by hobble bush, gooseberry, and blackberry; an herb layer dominated by *Eupatorium roanensis*, *Impatiens biflora*, and *Dryopteris dilatata*; and a ground layer represented by a light cover of certain species of mosses and lichens.

5. The spruce-fir community contains a tree layer dominated by spruce and fir with an addition of yellow birch at higher altitudes; a shrub layer dominated by purple rhododendron, blueberry, and hobble bush; an herb layer dominated by *Dryopteris dilatata* and *Oxalis acetosella*; and a ground layer heavily carpeted by mosses.

6. The balds, located along the linear summits of the mountain, cover approximately 1,000 acres. They are represented by three communities: (1) grassy balds, most extensive and found throughout the full extent of the bald area; (2) alder balds, confined essentially to the eastern end; and (3) rhododendron balds, confined principally to the western end of the summit.

7. The grassy bald represents the most homogeneous community, floristically, within the area studied. It is dominated by only one species, *Danthonia compressa* (mountain oat grass). Other frequent species are *Rumex acetosella*, *Agrostis hyemalis*, *Fragaria virginiana*, *Houstonia serpyllifolia*, and *Carex flexuosa*.

8. In the rhododendron bald, the shrub layer is dominated by an almost pure closed stand of purple rhododendron with only a light expression of species in herb and ground layers.

9. The alder bald consists of a shrub layer dominated by mountain alder and an herb layer of *Carex lucorum*, *Danthonia compressa*, and *Rumex acetosella*. These herbs find their best expression in the small openings between alder clumps.

10. The beech-maple community appears as an old and well stabilized climax for the zone it occupies, except in certain portions at the upper margin of its range where the spruce-fir appears to be gradually replacing yellow birch.

11. The theory of Indian origin of the grassy balds is discounted and the theory of natural origin sustained.

12. The grassy balds were once more extensive along the summit of Roan Mountain than at present, having given way to shrub and forest communities.

13. The spruce-fir forest community is climax for most of the area above 5,500 feet. It appears that under natural conditions the balds will eventually give way to this forest climax.

14. The recent advance of the coniferous forest into the grassy bald areas may possibly be caused by a change in climate, resulting in a less xeric condition for seedlings at critical times. Such climatic change is assumed to have been recent or is now in progress.

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AN OCEANOGRAPHIC CONSIDERATION OF THE
DINOFLAGELLATE GENUS CERATIUM

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	101
RELATIONSHIPS BETWEEN THE HORIZONTAL DISTRIBUTION OF CERATIUM AND CERTAIN ENVIRONMENTAL FACTORS	101
Salinity	101
Temperature	101
Nutrient Salts	105
Currents	106
Other Factors	107
CERATIUM LIFE ZONES IN THE AREAS TRAVERSED BY THE <i>Carnegie</i>	108
Region I: Cold North Atlantic	108
Region II: Warm Atlantic	108
Region III: Cold North Pacific	109
Region IV: Warm Pacific	110
Region V: Southeast Pacific	111
COMPARISON OF THE ATLANTIC AND PACIFIC WATERS ON THE BASIS OF THEIR CERATIUM FLORAS	111
THE VERTICAL DISTRIBUTION OF CERATIUM	113
SUMMARY	115
LITERATURE CITED	115

AN OCEANOGRAPHIC CONSIDERATION OF THE DINOFLAGELLATE GENUS CERATIUM

INTRODUCTION

In the course of the author's studies of the dinoflagellates (Peridineae) collected on the last cruise of the non-magnetic ship *Carnegie*¹ considerable material of an ecological nature was accumulated. This was particularly true of the common genus *Ceratium*, the study of which has now been completed. A taxonomic report of the genus embodying complete distributional records will be published by the Carnegie Institution of Washington in its volumes of reports on the scientific results of Cruise VII of the *Carnegie*. The present paper deals only with the ecological aspects of the genus. The dinoflagellate studies were conducted at the Hopkins Marine Station of Stanford University, Pacific Grove, California, during 1931-38, through the courtesy of W. K. Fisher, Director. The work was supported by the Carnegie Institution through J. A. Fleming, Director of its Department of Terrestrial Magnetism. Much of the microscopical work was accomplished with the assistance of Natalia Bronikovsky. Expert counsel was frequently given by T. Skogsberg of the Marine Station staff. To all of these the author wishes to express his deepest gratitude.

The *Carnegie* plankton collection contains almost all of the previously known species of marine *Ceratia* as well as three that are new, making a total of fifty-eight species. Since the *Carnegie* collecting extended from Iceland to Panama in the Atlantic and from

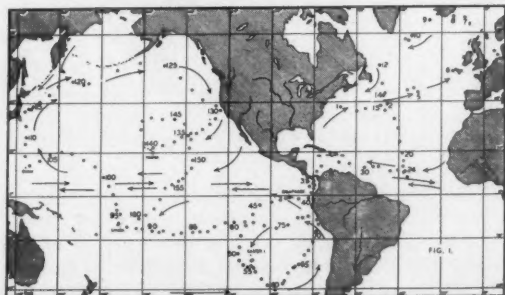


FIG. 1. Chart showing oceanographic stations occupied by the *Carnegie* during Cruise VII, 1928-29. Arrows indicate direction of general current movements.

the Aleutian Islands to 40° south latitude in the Pacific (Fig. 1), it was possible to make a study almost world-wide in extent of practically all of the marine *Ceratia* with comparable material.

¹ The *Carnegie* was built in 1909 by the Department of Terrestrial Magnetism of Carnegie Institution of Washington for the purpose of conducting a magnetic survey of the oceans of the world. On its last cruise (1928-29) oceanographic observations including the collection of plankton samples were added to its program of scientific investigation. The last cruise terminated upon the destruction of the vessel by fire in Apia, Samoa, November 29, 1929.

The oceanographic conditions observed included temperature, salinity, phosphate, H-ion concentration, silicate, dissolved oxygen, and currents. Each of these factors was examined in relation to the distribution of each species of the genus *Ceratium*. It is not feasible to give here a detailed account of the distribution of the environmental conditions throughout the area investigated, but these can be briefly summarized and discussed in relation to the distribution of *Ceratium* species.

RELATIONSHIPS BETWEEN THE HORIZONTAL DISTRIBUTION OF CERATIUM AND CERTAIN ENVIRONMENTAL FACTORS

SALINITY

In the regions investigated in the North Atlantic the surface salinities vary from 32.66 ‰ southeast of Greenland to 37 ‰ in the Sargasso Sea. In the North Pacific the salinity values are less than 33 ‰ north of the subpolar convergence, and rise to 35 ‰ in the tropics. In the South Pacific the values are mostly between 35 ‰ and 36 ‰ except in the region of Panama where they drop to 30 ‰.

It is probable that the slight variations in salinity found in oceanic waters have no influence on the distribution of *Ceratium* species. Peters (1934) could demonstrate no effect in the South Atlantic nor could Nielsen (1934) in the South Pacific except that in the region of Panama where the salinity is low the total number of species was unusually low. However, conditions there were also neritic so that this correlation with salinity was not necessarily significant. In the *Carnegie* investigations no correlation could be found between salinity and the distribution of any species of *Ceratium*.

TEMPERATURE

In the North Atlantic south of the subpolar convergence the surface temperatures are mostly above 20° C. (Fig. 2). There is an increase in temperature

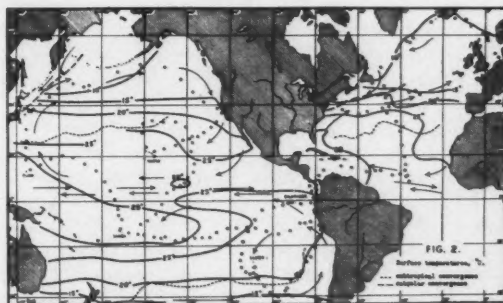


FIG. 2. Surface isotherms over the area traversed by the *Carnegie*. Isotherms computed from *Carnegie* data and data from Schott 1926 and Schott 1935.

southwestward to maxima above 28° in the Caribbean region. In the North Atlantic West Wind Drift the temperatures rapidly decrease to 11° and 12° toward the European continent. At the other stations, farther north, the surface temperatures are mostly around 10° C.

In the North Pacific there are six stations in water with surface temperatures less than 10° (Stations 119 to 124) south of the Aleutian Islands to the Kurils. Toward Japan there is a rapid increase in temperature southward so that there are only three stations in the transition zone between the cold northern water and the warm tropical water to the south. In the eastern Pacific, on the other hand, this transition is very gradual so that there are seven widely spaced stations between the 10° water south of the Aleutians and the 20° water of the tropics (Stations 125 to 131).

In the tropical regions of the Pacific the surface temperatures are mostly between 22° and 28° C. with the highest temperatures in the west. Temperatures



FIG. 3. Mean phosphate-content of upper 50 meters of water through areas traversed by *Carnegie*.

of less than 20° were recorded at two stations in the region of the Galapagos (Stations 42 and 43). The effects of the Humboldt Stream are apparent in a general lowering of the temperatures in the south-eastern Pacific region although temperatures as high as 25.27° were recorded off Peru. The *Carnegie* stations south of 20° south latitude are so far from South America that they do not show the severe effects of this current. Only three of the stations show temperatures less than 20° . Farther south, beyond 30° south, the effects of the southern West Wind Drift are very noticeable, with a fairly rapid reduction of the surface temperatures to 14.97° at 40° south at Station 60.

Peters (1934) came to the conclusion that water temperatures between 15° and 27.5° C. have no influence on the distribution of Ceratia in the South Atlantic. However, he was considering the yearly range of temperature at each locality. Peters did, on the other hand, group his species according to thermal environments. Of his 55 species, 33 were limited to warm water, 21 to warm and cool water, while only one was observed in the southern cold water. Nielsen (1934) was inclined to consider 15° C. too low for non-effective temperatures. However,



FIG. 4. Ceratium life zones as constructed on basis of studies of *Carnegie* Ceratia.

in the warm water regions which he investigated in the south Pacific he did not find many cases of temperature correlation. He designated only two temperate species, *C. Petersii* and *C. tripos atlanticum*; the rest were tropical. He also found that *C. flicorne* was restricted to high temperatures in the South Equatorial Current. In spite of so few temperature correlations, Nielsen did classify his species according to temperature zones with the following categories: tropical; tropical-subtropical; tropical-subtropical-temperate; and temperate.



FIG. 5. Chart showing relative numbers of species occurring throughout regions investigated by the *Carnegie*.

The geographic classification of species resulting from the study of the more extensive *Carnegie* material is a modification of Nielsen's and, of course, includes the cold water species as well as the tropical. It agrees with Nielsen's in recognizing the fact that most Ceratium species are tropical but that they differ in their distributions into temperate regions. The *Carnegie* classification differs from Nielsen's in that it recognizes no distinctively temperate species. All distributions are either fundamentally tropical, sub-polar, or cosmopolitan in character. Since the *Carnegie* passed into and out of the subtropical regions in both oceans, it was possible to study the transitions from tropical to cold water regions in four different places: in the western North Atlantic, western and eastern North Pacific, and eastern South Pacific. A comparison of species distributions in these regions gives valuable information regarding the limits of distribution of most of the species of the genus. For

such studies it is important to consider first the commonest tropical species so that negative records in the transition zones can be given some weight. *C. contortum* is an example of a common species with a typical tropical distribution (Fig. 6). The species

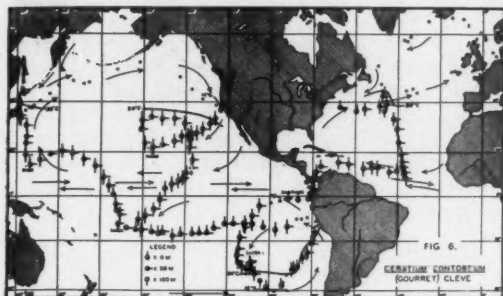


FIG. 6. Distribution of *C. contortum* (Gourret) Cleave at Carnegie stations.

drops out at surface temperatures of about 20° in the North Atlantic; at above 20° off Japan; 15° off California and 15° in the southeastern Pacific. Many other species have similar distributions, some more closely confined to certain temperatures, some less. *C. massiliense* (Fig. 7) is a common tropical species

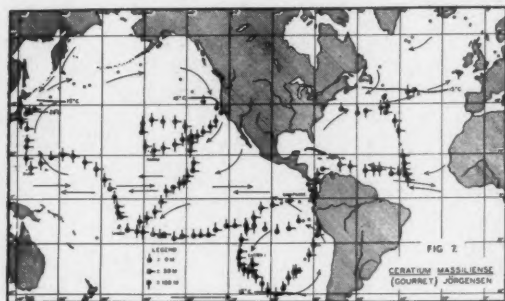


FIG. 7. Distribution of *C. massiliense* (Gourret) Jörgensen at Carnegie stations.

the limits of distribution of which parallel rather closely the 15° C. isotherms in the four transition zones. Some species show a definite restriction to tropical water except for a particular displacement by a current. A good example of this is *C. hexacanthum* (Fig. 8) which is within the 20° isotherm at the three transitions in the Pacific but in the Atlantic is apparently carried by currents to Iceland where the surface temperature is less than 10°. Conversely, there are species which are very restricted to warm water throughout their ranges. Examples of these are *C. breve* (Fig. 9) and *C. lunula* (Fig. 10).

A few species were restricted to cold water or were found only in insignificant numbers outside of cold water regions. *C. arcticum* (Fig. 11) is an example. Still a third general type of distribution is found in such species as *C. fusus* (Fig. 12) which occur as well in cold water as warm and are truly cosmopolitan.

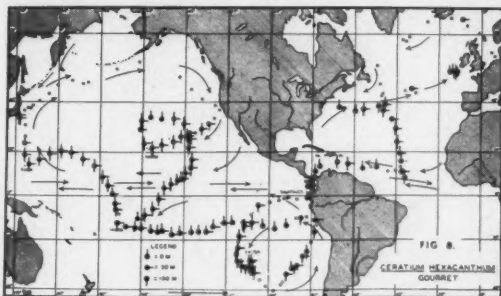


FIG. 8. Distribution of *C. hexacanthum* Gourret at Carnegie stations.

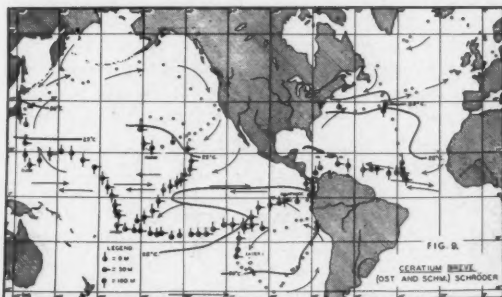


FIG. 9. Distribution of *C. breve* (Ost. and Schm.) Schröder at Carnegie stations.

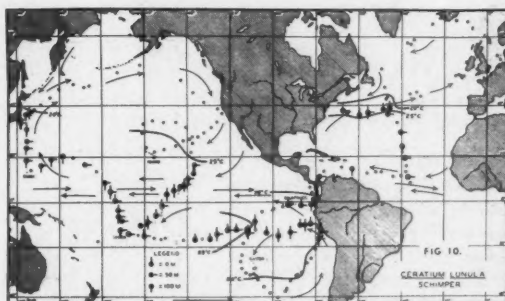


FIG. 10. Distribution of *C. lunula* Schimper at Carnegie stations.

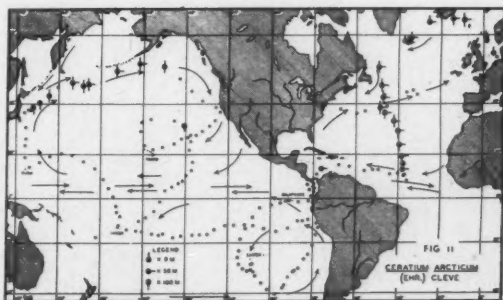


FIG. 11. Distribution of *C. arcticum* (Ehr.) Cleave at Carnegie stations.

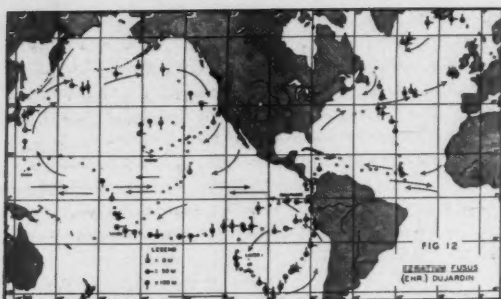


FIG. 12. Distribution of *C. fusus* (Ehr.) Dujardin at Carnegie stations.

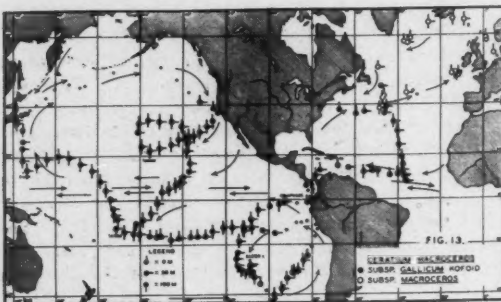


FIG. 13. Distribution of subspecies of *C. macroceros* at Carnegie stations.

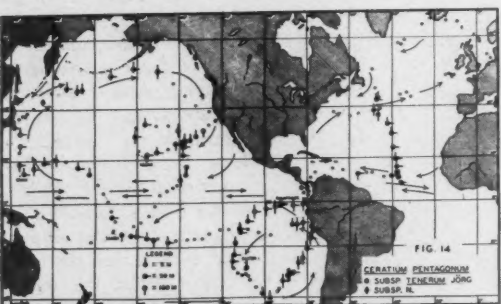


FIG. 14. Distribution of subspecies of *C. pentagonum* at Carnegie stations.

These correlations between the distributions of *Ceratium* species and the variation in temperature throughout the oceans do not necessarily indicate a causal relationship, as will be pointed out later. However, since correlations between environmental conditions and species distributions were best in the case of temperature, it seems justifiable to make the geographic classification on the basis of temperature for the present at least. Such a classification recognizes three main groups of species: tropical, subpolar, and cosmopolitan. The tropical species, in turn, are grouped into three subgroups: intolerant tropical, slightly tolerant tropical, and very tolerant tropical. The last two groups agree in general with Nielsen's tropical-subtropical, and tropical-subtropical-

temperate. The intolerant tropical species are rather closely restricted to regions with surface temperatures of 19° C. or over; the slightly tolerant tropical species migrate a little into the transition zones; while the very tolerant tropical species may be carried far beyond the tropical regions.

This classification has no category for temperate species. In this feature it differs from those previously used. According to the present investigations there are no truly temperate oceanic species of *Ceratium*. The temperate latitudes are populated with tropical and cosmopolitan species and occasionally with subpolar species. Following is the geographic classification of the *Carnegie* Ceratia based on the proposed scheme.

INTOLERANT TROPICAL

- C. incisum* (Karst.) Jörg.
- C. longirostrum* Gour.
- C. inflatum* (Kof.) Jörg.
- C. falcatum* (Kof.) Jörg.
- C. praelongum* (Lemm.) Kof.
- C. cephalotum* (Lemm.) Jörg.
- C. digitatum* Schütt
- C. belone* Cleve
- C. Bigelowii* Kof.
- C. breve* (Ost. and Schm.) Schröd.
- C. euvacuatum* Jörg.
- C. limulus* Gour.
- C. paradoxides* Cleve
- C. vultur* Cleve
- C. longissimum* (Schröd.) Kof.
- C. reflexum* Cleve
- C. deflexum* (Kof.) Jörg.
- C. lunula* Schimper
- C. filicorne* Nielsen
- C. trichoceros* (Ehr.) Kof.
- C. geniculatum* (Lem.) Cleve
- C. humile* Jörg.
- C. axiale* Kof.

SLIGHTLY TOLERANT TROPICAL?

- C. subrobustum* (Jörg.) Nielsen
- C. teres* Kof.
- C. Kofoidii* Jörg.
- C. gravidum* Gour.
- C. pulchellum* Schröd.
- C. symmetricum* Pav.
- C. declinatum* Karst.
- C. gibberum* Gour.
- C. concilians* Jörg.
- C. platycorne* Daday
- C. ranipes* Cleve
- C. carriense* Gour.
- C. tenue* Ost. and Schm.
- C. contrarium* (Gour.) Pav.
- C. macroceros* subsp. *gallicum* (Kof.) Jörg.
- C. pentagonum* subsp. *tenerum* Jörg.
- C. candelabrum* (Ehr.) Stein
- C. contortum* Cleve
- C. tripos* subsp. *aemipulchellum* (Jörg.)
- C. setaceum* Jörg.

VERY TOLERANT TROPICAL

- C. azoricum* Cleve
- C. massiliense* (Gour.) Jörg.

* Does not include three new species described in the unpublished report.

C. arietinum Cleve
C. extensum (Gour.) Cleve
C. hexacanthum Gour.

COSMOPOLITAN

C. horridum Gran
C. fusus (Ehr.) Duj.
C. furca (Ehr.) Duj.
C. tripos subsp. *atlanticum* Ost.
C. Petersii Nielsen³

SUBPOLAR

C. lineatum (Ehr.) Cleve
C. macroceros subsp. n.
C. pentagonum subsp. n.
C. arcticum (Ehr.) Cleve
C. compressum Gran³

NUTRIENT SALTS

Since the nutrient salt-content of seawater is known to be important in the total production of the phytoplankton, it is necessary to examine the variation in nutrients as a possible factor in the distribution of individual species of the photosynthetic genus *Ceratium*. Phosphorus and nitrogen are the most important plant foods in this respect. Only phosphate data are available for a discussion of the oceans as a whole but since the variations in quantities of phosphate and nitrate are usually parallel, a description of phosphate distribution will suffice to give a general picture of the distribution of phytoplankton foods in the areas investigated by the *Carnegie*. The discussion that follows deals with values which are the means of observed phosphate values for the surface and 50 meters, from *Carnegie* data (Fig. 3).

The warm North Atlantic waters are practically devoid of phosphate to 40° north latitude. North of 40° the mean values for the upper 50 meters are practically everywhere between 25 and 75 mg. PO₄/m³.

Most of the great area of the North Pacific between latitudes 10° and 38° north is practically devoid of phosphate, with values less than 10 mg. The cold waters to the north are very rich in phosphate. At the subpolar convergence northeast of Japan the phosphate-content rapidly increases northward and attains values above 100 mg. These high concentrations of phosphate continue eastward to longitude 150° west where they begin to drop off gradually southward. This southward gradient is in the California Current. Close off California values are between 25 and 75 mg. Farther out there is a rapid decrease to the very low values of the "Sargasso Sea of the Pacific." The North Equatorial Current lies in this area of extremely low phosphate-content.

Nowhere to the south of this current in the Pacific is there an area devoid of phosphate. The area of lowest phosphate-content in the South Pacific is in the Easter Island Eddy. However, at only two stations there do the values fall below 10 mg.

The subantarctic waters of the South Pacific West Wind Drift are very rich in nutrient salts. The

effects of this are shown by phosphate values above 50 at *Carnegie* Stations 60 and 61 at about 40° south latitude. Values over 100 mg. were found along the Peruvian coast, probably representing the combined effect of the Humboldt Current and local upwelling. In the general region between Peru and the Galapagos Islands and in the Panama region the values are above 50 mg. In the South Equatorial Current and its offshoots to the south the mean phosphate values for the upper 50 meters are mostly between 25 and 50 mg. as far west as Samoa.

The relations of these differences in the fertility of different regions to the planktonic flora is an interesting problem although a difficult one to investigate in a world survey since there is definitely a relation between high nutrient-content and low temperature. However, the following relationships are known.

In general, regions of very low phosphate-content are characterized by sparse populations of each species but by a large number of species; while regions of high concentrations of nutrients, characterized by few species, have great populations of those few species. The correlation between quantity of plankton and nutrient salt-content in the *Carnegie* data has been shown previously (Graham, 1933). The correlation between numbers of species and phosphate-content is amply shown by a study of the *Carnegie* material. In the northern part of the North Atlantic where the phosphate-content of the upper 50 meters is above 25 mg. PO₄/m³ the number of *Ceratium* species is less than 10 per station (Figs. 3 and 5). In the tropical Atlantic waters, on the other hand, where the phosphate-content is under 10 mg. the number of species of *Ceratium* per station is everywhere above 10, usually above 20, and at one station above 30. Likewise in the Pacific the phosphate-rich regions are characterized by a poor *Ceratium* flora. In the cold northern Pacific waters where the phosphate values are above 25 mg. and at most stations above 100 mg., the number of species per station is less than 10. The correlation is not quite so good in the warm tropical Pacific. There the number of species per station is between 20 and 30 throughout most of the region, although the phosphate-content of the northern part is under 10 mg. while in the southern part it varies from 10 to 50 mg. In the southeastern Pacific there are many values above 50 mg.; that is, higher than the warm region to the west. Accordingly, the number of species per station is less, between 11 and 20.

Thus, within any given area there seems to be a correlation between high phosphate-content and small number of species. This has been known for some time and it led Peters (1934) to suggest that high concentrations of phosphate and nitrate inhibit the growth of certain species of *Ceratium*.

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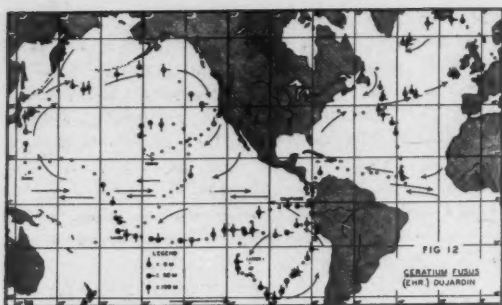


FIG. 12. Distribution of *C. fuscus* (Ehr.) Dujardin at Carnegie stations.

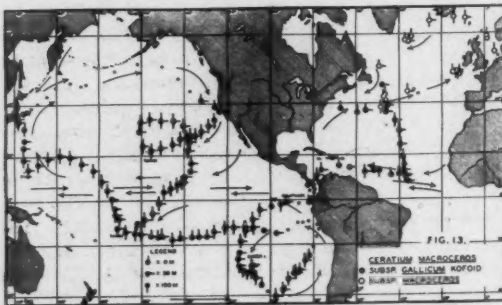


FIG. 13. Distribution of subspecies of *C. macroceros* at Carnegie stations.

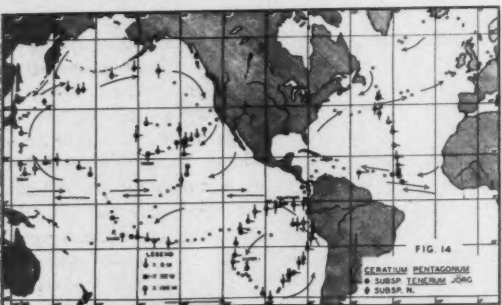


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area with more than 20 species includes water with over 25 mg. PO_4/m^3 . Similarly, in the North Pacific all the water containing more than 50 mg. PO_4/m^3 has less than 10 species per station while in the south-eastern Pacific there are areas where the phosphate-content is above 50 and the species per station are between 10 and 20.

To summarize, in the *Carnegie* data there is, in any particular large oceanic area, a negative correlation between the relative concentration of phosphate in the photic zone and the number of species of Ceratium found. When two large areas are compared this correlation does not hold for the absolute quantity of phosphate present. Thus, it is indicated that the absolute quantity of phosphate does not determine the number of Ceratium species occurring in a particular area. It is possible that the correlation with relative concentration in a limited area may be explained by assuming that some factor associated with an increase in phosphate is significant. Such an increase may be effected, for example, by upwelling. If some substance, not measured, were present in the deeper levels and acted to inhibit the growth of certain species, a correlation between the number of species and the concentration of phosphate relative to the surrounding area would result, since higher concentrations of phosphate are characteristic of deep water. It must be emphasized that the existence of any such substance is purely speculative.

CURRENTS

The main currents of the oceans investigated are indicated on all the accompanying charts. For a discussion of these see Schott (1926, 1935).

Currents are certainly important in the distribution of Ceratia. They cause displacements in the normal distribution by carrying populations into regions where they have not developed and they create displacements of the normal range of environmental conditions so that species can develop in regions which would otherwise not be favorable for them. The current factor in distribution is the most difficult one to demonstrate by a gross world survey such as that of the *Carnegie*. The value of Ceratia as current indicators is undoubtedly much greater than the *Carnegie* data indicate. The importance of such indicators is evidenced most in temporary current anomalies which can be observed satisfactorily only by a continued study of a particular area.

It should be emphasized that a current which displaces a flora from its normal distribution also displaces the environmental conditions. When the displaced water mixes with the adjacent water it may no longer be suitable for the organisms displaced and they disappear. That the amount of mixing in such currents is great, is indicated by the rather sharp delimitation of many of the Ceratium species in the *Carnegie* collection within a well-developed oceanic stream. This is particularly striking in the Kuro Sio and Gulf Stream, two currents well known for their velocity and general influence. In these the tropical

floras change their facies rather rapidly when the surface temperatures drop below 19° C.

Peters (1934) considered that ocean currents played a very great role in the distribution of Ceratia in the South Atlantic. However, he was able to give comparatively few instances of displacements of species in the areas he studied.

We tend to agree with Gran (1912) that the nature of a Ceratium flora is determined more by the chemical-physical conditions of the water than by transportation by currents. The fact that a warm current carries a tropical flora into high latitudes is not opposed to this argument as present evidence indicates that such a current will do this principally by carrying the tropical environment with it.

In the *Carnegie* investigations there were four regions where examples of current influences would be expected. These concerned four great currents: Gulf Stream, Kuro Sio, California Current, and Humboldt Current.

In the North Atlantic West Wind Drift or "Gulf Stream" the intolerant tropical species drop out at about 45° north. However, some of the tolerant tropical species show displacement. Thus, *C. extensum*, a tropical species, occurred as far as the British Isles in temperatures of 12.44° C. and *C. hexacanthum* to Iceland in temperatures of 8.92° C. These distributions are unquestionably examples of current displacements as *C. extensum* was not found elsewhere in temperatures below 14.97° nor *C. hexacanthum* below 18.97°. The occurrence of *C. massiliense* and *C. platycorne* off Ireland should probably also be considered displacements. Other tropical species such as *C. declinatum* and *C. ranipes* were carried northward only as far as Station 3 where the surface temperature was 15.5° C.

In the corresponding current of the Pacific, the Kuro Sio, the transition from tropical to subpolar floras was found to be more abrupt. Most of the tropical species were not carried into water with temperatures under 20° C. Only *C. gravidum*, *C. candelabrum*, and *C. tripos semipulchellum*, of the tropical species, were carried into water with surface temperatures as low as 15.93° C. No tropical species were found in this region in temperatures lower than 15.93° C.

Corroboration of the almost complete lack of displacement in the Kuro Sio was found in the distribution of tropical species at similar latitudes in the eastern Pacific off California. If currents are effective in displacing environments, then tropical species should be found in colder water off Japan than off California. The Kuro Sio should sweep populations into cold water and the California current push the northern limit southward. This was seldom found. The species which disappeared at 19° C. off Japan reappeared at 19° C. off California. There were many variations between species but in the main the tropical flora of the North Pacific had its northern limits in the eastern and western Pacific at the same isotherm and this isotherm was at approximately the same latitude, 40° north.

In the case of intolerant tropical forms, distributions were sometimes much more restricted. The distributions of *C. breve* (Fig. 9) and *C. lunula* (Fig. 10) are extreme examples of this. These species were found rather consistently within tropical latitudes, that is, within 20° of either side of the Equator. The ranges of these species beyond these latitudes, however, did not follow that of other common tropical species which are usually found throughout the warm water regions to about 40° north and south. In the case of *C. breve* the records do not extend far north or east of Hawaii although in the western Pacific they extend to Japan. They were absent from a large part of the southeastern Pacific, although they extended to Easter Island. The distribution of *C. lunula* was still more uneven in the North Pacific. In the east it was found nowhere north of 20° while in the west it was found continuously to northern Japan, latitude 38° north. In the South Pacific, however, it was everywhere within 20° south latitude. Is it possible that these distributions are determined by current systems? Certainly they cannot be accounted for by simple current displacements as a bodily displacement of the plankton would have displaced other species as well. May these curious distributions be the result of a specific susceptibility to something? Is the absence of these species in the southeast Pacific due to some deleterious effect of the outwash of subantarctic and upwelled water from the south and east, and is their absence from the region between California and Hawaii due to the combined effects of the California Current and upwelling?

Answers to these questions cannot be given until further work is done. It is remarkable that only two species show such distributions. Proof of the representative nature of the observations, of course, must await further investigations.

Equatorial currents apparently have little effect on the distribution of Ceratia. This is probably because they involve the movements of waters of very similar nature. Although temperatures of such waters may vary from 20° C. to 29° C., the surface temperatures above 20° C. apparently have no effect on the Ceratia. Nielsen found that *C. flicorne* was found only in the warmest parts of the South Equatorial Current but this was not corroborated by Carnegie data. No segregation of Ceratium species within the equatorial regions could be made on the basis of temperature.

The last great current system to be considered is the Humboldt Current off South America. Unfortunately, the Carnegie stations did not run near the continent except at Callao so that the most highly developed part of the current system was not encountered. The hydrography of the region off South America is complicated by a strong upwelling along the coast. The changes in the environmental conditions brought about by this upwelling are probably the same as those effected by the Humboldt Current which brings water from the subantarctic. These consist of lowered temperature and pH, increased phosphate, etc., with resultant increase in plankton production. Thus, it is impossible to decide whether

the biological conditions peculiar to this region should be attributed to current phenomena or to the other hydrographic feature, upwelling.

Probably there is a displacement by the Humboldt Current of Antarctic species northward along the southern part of the South American coast southeast of the Carnegie track but no evidence of this was observed at any Carnegie station. Probably the only antarctic form of Ceratium is *C. pentagonum robustum* (Peters, 1934). This did not occur in the Carnegie collection.

The Humboldt Current is deflected westward and there is a more or less general movement of water away from the South American coast in the southeastern Pacific. The effects of this westward movement of water are reflected in the chemical composition of the water for hundreds of miles toward the central Pacific. The biological conditions, also, are peculiar for hundreds of miles off shore: (1) there is a high production of total plankton; (2) there is a reduced number of Ceratium species (Fig. 5); and (3) the development of some tropical species apparently is suppressed.

Many tropical species common in the waters to the west were absent in at least certain parts of the southeastern Pacific. Sometimes such a distributional hiatus was confined to the Peruvian coast and Galapagos area as in *C. extensum* and *C. tenue*. Other species seemed to show a more or less general avoidance of the area as, for example, *C. pulchellum*, *C. carriense*, *C. vulture*, and *C. teres*.

Here again one is probably not confronted with a problem of simple current displacement but rather with current effects brought about through a modification of the environment. What these peculiar modifications might be will be discussed in the next section.

OTHER FACTORS

Although the above geographic classification of Ceratia (p. 104) has a temperature connotation, it does not necessarily signify that the controlling factor in Ceratium distribution is temperature. There are still other factors which are associated with temperature which have not yet been discussed.

For example, the silicate-content of the water must be considered in connection with the growth of diatoms. The Carnegie records for silicate as well as hydrogen-ion concentration were examined in connection with Ceratium species distributions but no correlations were found except inasmuch as they agreed with temperature correlations.

Nielsen (1934) is of the opinion that the concentration of plankton organic metabolic products is the most important factor in the distribution of Ceratium species in warmer seas. Since no measurements of such substances are available it is impossible to test this theory. Nielsen bases his opinion principally on the distribution of neritic and oceanic species and on the relative number of species in these two environments. He emphasized the fact that in neritic waters only a small number of Ceratia occur. That this is not due simply to higher concentrations of nutrients

was shown by distributions in the Great Barrier Reef Region where nutrients as well as Ceratium flora were low. Nielsen found higher concentrations of nutrients in the open ocean (eastern South Equatorial Current) with a diminution in species. He contended that the metabolic products require considerable time for decomposition; that the fertility of neritic water is replenished from shallow depths where these products have accumulated while in oceanic regions no such accumulation can occur. What these metabolic products are remains to be demonstrated. Even if the presence of such products is demonstrated and correlations are found, their causative nature must be proven and this probably will have to be done experimentally.

The difficulties in establishing the important environmental conditions are accentuated by the fact that many water conditions change together. The agency which enriches the photic zone to any great degree is a movement of water from deeper levels to the surface layers. This one agency, whether near shore or in the open ocean, brings about a whole set of new environmental conditions. Not only is the phosphate and nitrate-content of the water increased but the temperature is lowered and the hydrogen-ion concentration is increased. Undoubtedly other changes are effected also. If some particular metabolic product is rather stable, as Nielsen postulated, no doubt higher concentrations of this accompany any enrichment of the photic zone. A point worth considering in this connection, however, is that Nielsen's postulated metabolic product poisoning may be purely of plant origin. In this connection Hardy and Gunther's (1935) discussion of the "exclusion effect" of phytoplankton for zooplankton is interesting. There is considerable evidence accumulating that phytoplankton exerts an exclusion effect on many animals. Is it possible that it may in a similar way exclude certain species of Ceratium?

The association of all these factors makes it difficult to select the particular one which might be influencing the distribution of any particular species. Thus, the floristic zones to be outlined are separated not only by certain temperature differences but by certain associated differences in phosphate, pH, plankton-content, etc.

The difficulty involved in determining causative factors is well illustrated in the waters of the southeast Pacific where obviously some condition associated with the Humboldt Current and upwelling limits the distribution of certain Ceratium species. The condition there is probably not temperature, as many of the temperatures are over 20°. However, which of the conditions associated with cold currents and upwelling is the determining one cannot be pointed out at this time.

CERATIUM LIFE ZONES IN THE AREAS TRAVERSED BY THE *Carnegie*

The areas traversed by the *Carnegie* can be divided into five regions on the basis of their Ceratium floras (Fig. 4). Each region is characterized by particular

hydrographic conditions. Two of the regions are in the North Atlantic, the Cold North Atlantic Region and the Warm Atlantic Region; three are in the Pacific, the Cold North Pacific Region, the Warm Pacific Region, and the Southeast Pacific Region.

REGION I

Cold North Atlantic (Stations 3-13)

This region includes the loop of eleven stations lying north of 40° north and extending to Iceland. The entire area is composed of eutrophic water with surface temperatures under 16° C. and phosphate-content of upper 50 meters above 25 mg. PO₄/m³. The Ceratium flora in this region is characterized by subpolar species as well as by tolerant tropical species which probably have been carried northward by the West Wind Drift and its tributaries. It is also characterized by a paucity of species, although the total population is relatively high. The number of species per station was 10 for two stations but less than 10 for other stations; sometimes as low as one or two. The total number of species found was only 14.

The following species were found at five or more of the 11 stations in the region. They are to be classified as either subpolar or cosmopolitan.

- C. arcticum*
 - v. *arcticum* at 6 stas.
 - v. *longipes* at 7 stas.
 - v. *ventricosum* at 5 stas.
- C. macroceros* subsp. *macroceros*
- C. furca*
- C. fusus*
- C. horridum* v. *horridum*
- C. lineatum*
- C. tripos* subsp. *atlanticum*

The following species were found at only one to three stations in the region. They are all tolerant tropical or cosmopolitan species.

- C. arietinum* subsp. *bucephalum*
- C. declinatum*
- C. hexacanthum*
- C. macroceros* subsp. *gallicum*
- C. ranipes*
- C. azoricum*
- C. extensum*
- C. horridum* var. *molle*
- C. massiliense*

No intolerant tropical species were found in Region I. The least tolerant species were *C. declinatum*, *C. macroceros* subsp. *gallicum*, and *C. ranipes*, and each of these was found at only one station in the southern limit of the region. Thus, the dominant flora of Region I is subpolar in character and a subdominant element is made up of tolerant tropical species.

REGION II

Warm Atlantic (Stations 1, 2, 14-34)

This region includes 23 stations, all of which lie south of 40° north latitude. The entire area is composed of water with surface temperatures above 20° C. The phosphate-content is extremely low every-

where except at the three northernmost stations. There the mean values for the upper 50 meters were from 14 to 52 mg. PO_4/m^3 . At the rest of the stations the values were 10 mg. or less. Consequently, except to the north, the region supports a very small quantity of plankton and is distinctly oligotrophic. The sparse plankton, however, is composed of a large number of species. This number was between 10 and 20 per station in the Caribbean Sea and western part of the North Equatorial Current but higher at the other stations; between 20 and 30 except at Station 16 where there were 33 species. The total number of species found in this region was 46.

The Ceratium flora in Region II is distinctly tropical with the usual number of cosmopolitan forms and a few subpolar occasional. The following species were found at 15 or more of the 23 stations. This list represents only intolerant and slightly tolerant species (*C. hexacanthum* and *C. massiliense*) and two cosmopolitan species (*C. macroceros* and *C. tripos*).

- C. breve*
- C. contortum*
- C. eucarvatum*
- C. gravidum*
- C. macroceros*
 - subsp. *macroceros* at 3 stas.
 - subsp. *gallicum* at 21 stas.
- C. tenue*
 - v. *inclinatum* at 17 stas.
 - v. *tenuissimum* at 7 stas.
- C. candelabrum*
- C. contrarium*
- C. gibberum*
- C. hexacanthum*
- C. massiliense*
- C. ranipes*
- C. tripos*
 - subsp. *atlanticum* at 8 stas.
 - subsp. *semipulchellum* at 19 stas.
- C. vultur*
 - v. *sumatranum* at 15 stas.
 - v. *Pavillardii* at 8 stas.
 - v. *japonicum* at 8 stas.
 - v. *vultur* at 11 stas.
 - v. *recurvum* at 10 stas.

The following species were found at from 5 to 14 stations. They consist of tropical and cosmopolitan species as well as one subpolar species.

- C. arcticum*
 - v. *arcticum* at 6 stas.
 - v. *longirostrum* at 6 stas.
 - v. *ventricosum* at 1 sta.
- C. carriense*
- C. extensum*
- C. fusus*
- C. limulus*
- C. lunula*
- C. pulchellum*
- C. reflexum*
- C. teres*
- C. trichoceros*
- C. arietinum*
 - subsp. *arietinum* at 4 stas.
 - subsp. *gracilentum* at 2 stas.

- C. declinatum*
- C. furca*
- C. horridum*
 - v. *horridum* at 5 stas.
 - v. *molle* at 9 stas.
 - v. *claviger* at 1 sta.
- C. paradozides*
- C. symmetricum*
 - v. *symmetricum* at 1 sta.
 - v. *coarctatum* at 9 stas.
 - v. *orthoceros* at 4 stas.

The following species were found at fewer than 5 stations in the region. This list comprises intolerant tropical species almost exclusively.

- C. azoricum*
- C. cephalotum*
- C. digitatum*
- C. humile*
- C. inflatum*
- C. longirostrum*
- C. subrobustum*
- C. belone*
- C. concilians*
- C. falcatum*
- C. incisum*
- C. lineatum*
- C. longissimum*

The relative frequency of the species in Region II was approximately the same as that for the collection as a whole so that no particular significance can be attached to it. The species which were rare in Region II were rare throughout the world and vice versa.

The southern part of Region II corresponds to the northern part of Peter's (1934) Region I of the South Atlantic. The composition of dominant species in the Carnegie material agrees with that of Peters.

The area with a low number of species per station from Station 26 to 34, including the Caribbean Sea (Fig. 5) cannot be considered biologically different except in its greater general poverty. The temperatures are higher there, all above 27° or 28° C., and the plankton generally sparse. Although the number of species per station is generally low throughout this area the total number for the area is not far below that for the entire Region II; 32 as compared with 46 for Region II. The species not represented are mostly rare ones. The data obtained in this area probably can be explained by a very poor production of all species resulting in the rarer species being seldom collected.

REGION III

Cold North Pacific (Stations 116-128)

This region includes 13 stations all but one of which lie north of 40° north latitude. The area is composed of cold eutrophic water with surface temperatures below 17° C. (as low as 7.15° at one station) and with phosphate-content of the upper 50 meters above 25 mg. PO_4/m^3 at all stations but one and above 100 mg. at the seven northernmost stations. Consequently, this region supports a dense growth of plankton although the number of species is small. This number was below 10 at all but one station.

The Ceratium flora in this region is characterized in general by a few subpolar and cosmopolitan species, while at the southernmost stations there were a few records of slightly tolerant and very tolerant tropical species.

The following species were found at more than 3 of the stations. They are all subpolar or cosmopolitan species.

- C. arcticum*
 - v. *arcticum* at 2 stas.
 - v. *longipes* at 9 stas.
- C. fusus*
- C. tripos*
 - subsp. *atlanticum* at 7 stas.
 - subsp. *semipulchellum* at 1 sta.
- C. arietinum*
 - subsp. *arietinum* at 6 stas.
 - subsp. *bucephalum* at 2 stas.
- C. pentagonum* subsp. n.

The following species were found at three or fewer stations in the region. They are subpolar, cosmopolitan, very tolerant and slightly tolerant tropical species.

- C. azoricum*
- C. carriense*
- C. contrarium*
- C. furca*
- C. horridum*
 - v. *horridum*
- C. macroceros*
 - subsp. *gallicum*
- C. massiliense*
- C. tenue*
 - v. *inclinatum*
- C. candelabrum*
- C. concilians*
- C. extensum*
- C. gravidum*
- C. lineatum*
- C. Petersii*

REGION IV

Warm Pacific (Stations 45-47, 63-66,
78-115, 129-160)

This region includes 87 stations covering the tropical Pacific extending to approximately 40° north and 35° south latitude except in the southeast Pacific where it meets the Southeast Pacific Region. Region IV is characterized by warm water with surface temperatures above 20° C. except at the borders of the region where it is lower, particularly off California where stations with surface temperatures as low as 16.3° have been included. The phosphate-content of the water in this region is not the same throughout. The central part of the North Pacific is practically devoid of phosphate with mean values for the upper 50 meters under 10 mg. PO₄/m³. At the northern limits of the region these values increase to 25 mg. The phosphate-content of the water in the southern part of Region IV is mostly above 25 mg. except in the Easter Island Eddy where it is between 10 and 25 mg.

Region IV is characterized by a large number of species of Ceratium per station although the total

plankton population is, on the whole, low. The numbers of Ceratium species per station are everywhere between 20 and 30 except for four stations near the Equator where they are over 30 and at the northern transitions where they are between 10 and 20.

The Ceratium flora of this region is distinctly tropical and includes all of the strictly tropical species as well as the tolerant ones and cosmopolitan and stray subpolar species.

The following species were found at more than 60 of the 87 stations in this region. This list is composed principally of slightly tolerant and very tolerant tropical species.

- C. candelabrum*
- C. contortum*
- C. declinatum*
- C. extensum*
- C. gravidum*
- C. macroceros* subsp. *gallicum*
- C. tenue*
 - v. *inclinatum* at 58 stas.
 - v. *tenuissimum* at 21 stas.
- C. carriense*
- C. contrarium*
- C. eucarvatum*
- C. gibberum*
- C. hexacanthum*
- C. massiliense*
- C. trichoceros*
- C. tripos*
 - subsp. *atlanticum* at 12 stas.
 - subsp. *semipulchellum* at 75 stas.

The following species were found at from 25 to 60 stations in the region. This list is composed mostly of intolerant and slightly tolerant tropical species.

- C. arietinum*
 - subsp. *arietinum* at 16 stas.
 - subsp. *bucephalum* at 15 stas.
- C. cephalotum*
- C. deflexum*
- C. furca*
- C. limulus*
- C. pentagonum*
 - subsp. *tenerum*
- C. platycorne*
- C. subrobustum*
- C. pulchellum*
- C. teres*
- C. Bigelowii*
- C. breve*
- C. concilians*
- C. falcatum*
- C. fusus*
- C. lunula*
- C. paradoxides*
- C. praelongum*
- C. symmetricum*
- C. ranipes*
- C. vultur*
 - v. *sumatranum* at 34 stas.
 - v. *regulare* at 1 sta.
 - v. *reversum* at 6 stas.
 - v. *Pavillardii* at 7 stas.
 - v. *vultur* at 16 stas.
 - v. *japonicum* at 18 stas.

The following species were found at fewer than 25 of the 87 stations in the region. This list, also, is composed principally of intolerant and slightly tolerant species.

C. arcticum v. *longipes*
C. axiale
C. belone
C. digitatum
C. geniculatum
C. incisum
C. inflatum
C. longirostrum
C. reflexum
C. setaceum
C. azoricum
C. flicorne
C. horridum
 v. *horridum* at 10 stas.
 v. *claviger* at 10 stas.
 v. *molle* at 7 stas.
C. kofoidii
C. petersii
 plus 3 new species

REGION V

Southeast Pacific (Stations 35, 36, 38-44,
 58-62, 67-77)

This region includes 25 stations in the southeastern Pacific from Panama to 40° south latitude and from the South American coast westward. It has two tongues extending westward, one to the north of and one to the south of the Easter Island Eddy. Although the temperatures vary a great deal in this area, the water is everywhere eutrophic. The observed surface temperatures varied from 14.97° C. at the southernmost station to 27.4° in the Panama Region. The mean phosphate-content of the upper 50 meters was everywhere above 25 mg. PO₄/m³ and was above 50 mg. at all stations except those bordering the Easter Island Eddy.

The waters of this region support a large plankton population and, characteristically, few species are present. Region V has been delimited by the points at which the number of species per station rises above 20. Not only is the number of species lower in this region than in the warmer tropical waters to the west but the composition of the Ceratium flora is somewhat different. The following tropical species found to the west were absent from Region V. They are, significantly, all intolerant tropical species.

C. axiale
C. digitatum
C. inflatum
C. reflexum
C. cephalotum
C. flicorne
C. longirostrum

The following species were found at 15 or more stations within the region. The list is composed mostly of cosmopolitan and tolerant tropical species.

C. candelabrum
C. furca

C. horridum
 v. *horridum* at 12 stas.
 v. *molle* at 5 stas.
 v. *claviger* at 4 stas.
C. contortum
C. fusus
C. tripos
 subsp. *atlanticum* at 10 stas.
 subsp. *semipulchellum* at 15 stas.
C. lunula
C. massiliense
C. pentagonum
 subsp. *tenerum*

COMPARISON OF THE ATLANTIC AND PACIFIC WATERS ON THE BASIS OF THEIR CERATIUM FLORAS

There is no known difference in the environmental conditions of the waters of the Atlantic and Pacific oceans which might operate to favor or hinder certain species in one ocean and not in the other. Given the same plankton communities it would be expected that the same species would survive in each. However, the two oceans are sufficiently isolated from each other that the same plankton communities have not developed in each. The two oceans are separated except in the south where they both merge into the Antarctic Ocean and in the far north where they are connected by way of the Arctic Ocean and narrow Bering Strait. For this reason a comparison of the plankton in the two oceans is of particular interest.

Judging from the geographic distribution of the tropical species of Ceratium there seems to be no doubt that cold water areas constitute in some way a barrier to the distribution, or at least the normal development, of most of the tropical species within each ocean. The problem now is, are such environmental barriers effective in confining species to a particular ocean or can the species pass freely from one ocean to the other?

Before examining the biological evidence connected with this problem one should examine the nature of the water connections between the oceans of the world. Considering first the northern connection it is significant that Bering Strait is shallow and narrow with maximum water temperatures never exceeding 8° C. (Schott, 1935). It is not likely that an organism could travel between the Atlantic and Pacific without passing through water of 0° C. or lower in the Arctic. For this reason it is fairly safe to assume that there is no passage of tropical species through these waters. This is substantiated by the fact that tropical species have not been found even as far north as the Aleutian Islands. It is very probable that, as far as tropical planktonic species are concerned, the North Atlantic and North Pacific oceans are effectively separated from each other. This is corroborated by the fact, as will be shown later, that even the cold water planktons of these two oceans do not indicate a communication.

Turning now to the far southern waters it is apparent that land masses are scarce. In this region oceanic water encircles the globe and makes broad connections with the Atlantic, Pacific, and Indian

oceans. For this reason the plankton of the Antarctic is identical with that of the most southern limits of the Atlantic, Pacific, and Indian oceans. The temperature of the far southern waters is very low and the question is, can the tropical species of the world pass from one ocean to the other by way of the subantarctic region? The highest surface temperatures attained in the latitude of Cape Horn in the southern summer are under 8° C. Whether this temperature is sufficiently low to constitute a barrier to the movement of tropical *Ceratium* species or their spores between the South Atlantic and South Pacific is problematical but from present knowledge it would be expected to represent such a barrier. In any case, the African continent must certainly constitute a less effective barrier between the South Atlantic and Indian oceans than the South American continent does between the South Pacific and South Atlantic since the temperatures at Cape of Good Hope in summer may be above 20° C. (Schott, 1926). There is no continental barrier between the Indian Ocean and the warm waters of the Pacific Ocean.

The Atlantic tropical waters are definitely not separated by any cold water area from the warm Indian Ocean and tropical Pacific toward the east but they are separated from the Pacific toward the west by the cold water at the tip of South America. Turning now to the currents in the far southern waters we find that there is a strong west wind drift carrying water from west to east. It would be expected that the Atlantic tropical plankton would be carried to the Indian and finally to the Pacific oceans but that the Pacific tropical plankton might not be able to find its way to the Atlantic to the east because of the low temperatures south of "The Horn." Under these conditions any planktonic species originating in the Pacific might never reach the Atlantic whereas species of Atlantic origin should in time be carried to the Indian and ultimately to the Pacific Ocean.

In the light of this knowledge it is interesting to compare the tropical *Ceratium* floras of the Pacific and Atlantic oceans. An examination of the *Carnegie* lists of species for the two oceans shows that most of the species are common to both oceans. However, there are some notable differences. In the *Carnegie* records nine of the species occurred in only one ocean and this, significantly, was the Pacific. One of these, *C. axiale*, has been found in the Atlantic by others so it will be disregarded. The others are as follows: *C. flicorne*, *C. Petersii*, *C. Bigelowii*, *C. deflexum*, *C. geniculatum*, and three new species.

None of the Atlantic species was absent from the Pacific. Nielsen in his comparison of the two oceans cites two examples of Atlantic species which are absent from the Pacific: *C. longinum* Karsten (= *C. arcuatum longinum* in Peters, 1934) and *C. minutum* Jörgensen. These species, however, have been found abundantly in the Pacific in the *Carnegie* collections. Otherwise, Nielsen's comparisons of the two oceans agree well with the *Carnegie's* except that Nielsen lists *C. humile* as absent from the Atlantic.

It is true, of course, that most of the species peculiar

to the Pacific are rare species and may yet be discovered in the Atlantic. However, in the case of at least three of the species: *C. Bigelowii*, *C. deflexum*, and *C. flicorne*, this is not likely as many records of their occurrences are now accumulating. In the *Carnegie* collection alone there are 37 sample records for *C. Bigelowii*, 105 for *C. deflexum*, and 27 for *C. flicorne*.

It should be noted that the eight species peculiar to the Pacific are strictly, or only slightly tolerant, tropical species, not occurring at stations where the surface temperature was less than 20° C. Thus, those species might find it impossible to pass around Cape Horn in the cold southern water.

It seems quite possible that the eight species above-mentioned have originated in the Pacific Ocean and must forever remain in the warm regions of that great ocean, being barred from the Atlantic by the great southern extension of South America, while the species that have originated in the Atlantic have found an easy migration to the Pacific by way of the Indian Ocean.

If this condition of "one-way migration" is correct then there should be no strictly planktonic tropical species of any kind in the Atlantic which does not also occur in the Pacific, whereas, many species should be found which are unique to the Pacific. Since this seems to be true for the genus *Ceratium* investigations should be conducted on many other groups of the tropical planktonic community with this point in mind.

Now compare the cold water floras of the northern Atlantic and Pacific. As has been stated, the connection between these two oceans to the north by way of the Arctic Ocean and Bering Strait contains water which never reaches a temperature so high as 8° C. and probably in some regions never much above 0° C. Is there a communication between the cold water plankton of the North Pacific and North Atlantic? In so far as the genus *Ceratium* is concerned, the evidence indicates there is not.

Although there are certain similarities between the *Ceratium* floras of the Cold North Pacific and Cold North Atlantic Regions, there are on the other hand some very striking differences which can be accounted for only on the assumption that these two oceans are biologically isolated from each other. The similarities in the two floras are expressed by the occurrence in both regions of the two subpolar species: *C. lineatum* and *C. arcticum*.

The differences in the floras of the two regions are more striking than the similarities. In contrast to the tropical floras these differences are not one-sided. "Mono-oceanic" species are not all in one ocean so that, in contrast to the southern oceans, a mutual isolation is indicated.

The significant examples in this case are subspecies rather than species. The first of these to consider is *C. furca*. This species broadly considered is cosmopolitan. However, it was noted that in the Atlantic there was a hiatus between the tropical records and the cold water records. Although no morphological

difference could be discerned between the southern and northern forms it was suggested that they represented at least physiological subspecies. In the Pacific the species is represented only in the warm water regions except for one station in Region III off Japan, which must be considered a displacement by the Kuro Sio. The species is absent along the rest of the cold water area of the Pacific traversed by the *Carnegie*. From this it seems probable that the tropical Pacific form can be identified with the tropical Atlantic form and that the northern Atlantic form represents a subspecies which is absent from the cold northern Pacific waters.

The case of another species, *C. macroceros*, is somewhat more convincing inasmuch as the subspecies are morphologically easily distinguishable. Subspecies *gallicum* is characteristic of all warm water regions. It is widespread over both the Atlantic and Pacific. The species is represented in the cold North Atlantic by subsp. *macroceros*. In the cold North Pacific, however, the species is conspicuously absent (Fig. 13). An assumption of the isolation of the North Pacific based on these two examples alone is not very conclusive since it is based on negative evidence in a region not well investigated, the North Pacific. The following example, however, does not carry this weakness and, taken with the foregoing two examples, forms convincing evidence of the isolation of the northern waters of the North Pacific.

This example is *C. pentagonum*, a widespread tropical species. Peters (1934) found a cold water subspecies in the subantarctic waters of the South Atlantic, subsp. *robustum*, the most southern representative of the genus. He emphasized the remarkable absence of any representative of the species in the cold waters of the North Atlantic. The absence of the species in these waters is well established as the region has been thoroughly investigated by many workers. The *Carnegie* investigations in the North Pacific revealed a very divergent new subspecies⁴ which was found only in the cold waters of the North Pacific (Fig. 14). It attained a high degree of morphological distinctness in the coldest water although it intergraded with var. *tenerum* at its southern limits. There can be no doubt that the new subspecies is not found in the Atlantic and is peculiar to the cold waters of the North Pacific.

These three striking differences in the Ceratium floras of the cold regions of the two oceans indicate that a barrier to at least some of the subpolar species exists between these two water masses. The nature of this barrier, of course, is only a matter for speculation. At Bering Strait there is a strong movement of water northward from Bering Sea to the Arctic Ocean at least during the summer months (Barnes and Thompson, 1938). This movement apparently does not result in a successful transplantation of all the Ceratium species from the cold North Pacific to the Atlantic. Possibly some feature of Arctic Ocean conditions acts as a barrier. Hydro-

biological investigations in the Arctic should throw some light on this problem.

THE VERTICAL DISTRIBUTION OF CERATIUM

Karsten (1907) was the first to point out that certain marine phytoplanktons live in the lower boundary of the photic zone where illumination is extremely low. He designated certain diatoms belonging to the genera *Coscinodiscus*, *Planetoniella*, and *Gossleriella* as constituting a "shade flora." Also, he thought that the genus *Ceratium* was represented at different levels by different species or varieties and designated *C. gravidum* Gourret, *C. tripos azoricum* Cl. var. *breve* Ost., and *C. tripos gibberum* Gourret as shade species. As Nielsen (1934) stated, an inspection of Karsten's lists does not corroborate his conclusions concerning *Ceratium* except in the case of *C. gravidum*.

Schröder (1911) listed *C. inflexum* f. *claviceps* (= *C. contrarium* f. *claviceps*), *C. platycorne*, and *C. limulus* as species which "avoid" the intense continued sunlight of the "southern waters."

Jørgensen (1920) made an intensive study of the vertical distribution of *Ceratium* in the Mediterranean. He found that a great number of species which occurred at the surface in winter inhabited the deeper levels in summer. He concluded that this flora is regularly carried into the Mediterranean from the Atlantic in winter and that it is replaced at the surface in summer by a flora indigenous to the Mediterranean. Paulsen (1931) and Nielsen (1934) challenged this migration theory of Jørgensen but Böhm (1931) accepted it. Peters (1934) could not establish any vertical distribution from the material of the *Meteor* expedition.

Nielsen (1934) reporting on the *Dana* collections, found that about one third of the *Ceratium* species occurring in the southern Pacific Ocean should be designated "shade species" while the rest of the species inhabit predominantly the upper layers. He found that the density of the plankton affects the vertical distribution of the shade species. These species occur in higher levels in the richer water, presumably because in such regions there is not sufficient light for growth at the lower levels.

Nielsen (1934) compared the shade species of *Ceratium* with the shade plants of the tropical rain forest all of which have their leaf surface increased in some way. The leaves are thin and there is an increase in assimilating cells. So in *Ceratium* the cells are thin and crowded with chromatophores. The cell body (and apical horn) may be expanded and crowded with chromatophores (chloroplasts) as in *C. gravidum*, or the antapical horns may be expanded and chloroplast-rich as in *C. platycorne*, *C. claviger*, and *C. ranipes*.

Long-horned species are found as well among shade species as among surface species but the shade species always have thin-walled horns, which are crowded with chromatophores.

Among the surface species there is not a single example of surface expansion. The usual assumption

⁴ For nomenclatural reasons the name will not be given in this report.

that surface expansion in *Ceratium* is a flotation adaptation is erroneous.

Since the *Carnegie* plankton collection contains samples collected at 50- and 100-meter depths as well as at the surface, and since the collection contains practically all the marine species of the genus, it was possible to test the theory of Nielsen in the case of each species. Although the *Carnegie* collecting nets were open nets, the duration of towing at the standard level was so much greater than the time of hauling in that the percentage of "contaminants" was necessarily small. These contaminants are upper-level species so that they do not introduce any error into the calculations in the case of deeper dwelling species.

For each species reported in the *Carnegie* collection the number of records for each collecting level was computed. Since there were more surface hauls than deeper hauls, these numbers required weighting. Consequently, they were computed as percentages of the total number of samples collected at the particular depth. Tables were compiled showing these values as well as the actual number of records for the three levels. Since an expression of the relative abundance of the species at each level is more significant than the mere positive record, the number of records of "rare," "occasional," etc., and their percentages were computed as well as the total number, and these were included in the tables.

Such an analysis of the *Carnegie* distributional records showed that 20 of the species were definitely more abundant in the deeper levels and 9 were questionably so. Each of the 20 species showed an increase in frequency from surface to 100 meters. The agreement between these species and the species indicated as "shade-species" by Nielsen is very great (Table 1).

There are only three cases of definite disagreement. Nielsen classified *C. subrobustum* and *C. trichoceros* as surface species while the *Carnegie* data indicate definitely that they are shade species. On the other hand, Nielsen indicated *C. hexacanthum* as a shade species while the *Carnegie* data failed to substantiate this. The agreement between the *Carnegie* and *Dana* shade species and the "winter species" of Jørgensen (1920) is also great. Only one of Jørgensen's winter species, *C. Kofoidii*, has been classified as not a shade species by both Nielsen and the present author.

What are the ecological advantages of shade species of *Ceratium*? In the summer time the upper levels of the sea are depleted of nutrient salts to a depth equal at least to that populated by the phytoplankton. Obviously, the species of phytoplankton which are most tolerant of shade have a decided advantage in the quest for nitrogen and phosphorus which occur in the deeper levels in large quantities. The poverty of nitrogen and phosphorus which land plants everywhere are enduring is accentuated to a high degree in the ocean. When a land plant dies its nitrogen and phosphorus are soon returned to the soil to be utilized by other plants. On the other hand, when a planktonic plant dies it sinks below the photic zone

and its nutrient elements are lost, to be returned only after a long period of time except in high latitudes and in certain peculiar regions. This is particularly true of the tropics where the thermal stratification is extreme and continuous. In these regions it is probable that the fertilization of the photic zone is accomplished primarily by the nocturnal visits of a sparse zooplankton. It is in such regions as this that the shade species of *Ceratium* develop. Nielsen (1934) has already observed that the shade species are all warm-oceanic; they do not occur in neritic conditions nor in the cold water southeast of New Zealand. The *Carnegie* observations show that none of the shade species are cold water species, with the possible exception of *C. arcticum* and *C. horridum*. Of the 29 species definitely or questionably shade species according to *Carnegie* data, 17 are intolerant tropical species, 8 are slightly tolerant tropical species, only 2 are very tolerant tropical species, one is cosmopolitan (*C. horridum*) and one subpolar (*C. arcticum*).

The data concerning the depth at which *C. arcticum* lives most abundantly are not conclusive but they suggest that it is a shade species. *C. arcticum* is a cold water species and may represent a type with ecological relationships different from that of the tropical species. Shirshov and Fedorov (1938) have found phytoplankton flourishing under the arctic ice. They have not yet reported the species found but probably *C. arcticum* is one of them as it is characteristic of arctic currents. In the low illumination occurring under the ice it would be expected that only species with high tolerance for shade would be found. The nutrients here are rich. These species when living in exposed ice-free regions would then have the advantage of the ability to live at greater depths than the species not tolerant of shade so that they would be found at depths equal to that of the tropical shade species. This may be the explanation of the larger number of records of this species at subsurface levels in the lower latitudes.

The occurrence of shade species of *Ceratium* near the surface in the Mediterranean in winter (Jørgensen, 1920) prompted Nielsen (1934) to postulate a phototropic response for these species. He assumed that the species in winter when the light intensity is low come to the surface and thus are able to maintain a position in optimal light intensity.

The variation in the vertical distribution of *Ceratium* throughout the year in the Mediterranean may be due in part to a phototropic response on the part of individual organisms but certainly a simple phototropism cannot explain the general distribution of *Ceratium* shade species. In the *Carnegie* collection, the shade species were found most abundantly at 100 meters. The light intensity at this depth even in summer cannot be compared with the light intensity at the surface in winter in the Mediterranean nor, indeed, in any part of the world. It is scarcely logical to assume on the basis of the present data that the shade species of *Ceratium* seek a zone of a particular light intensity.

Although migrations among these motile microscopic organisms may play a part in their dis-

tributions the occurrence at a given level does not necessarily indicate the organisms' ability to seek and remain at that level. Greater abundance at a certain level may be the result of greater development at that level due to more favorable environmental conditions obtaining at that level.

The predominance of a certain species is usually the result of that species being better adapted to the particular environmental conditions than are other species. The occurrence of shade species at levels of low illumination would indicate that these species are better able to develop under such conditions than are other species. Quite possibly the shade species would develop abundantly at the surface if it were not for the antibiotic effect of surface species which are better able to take advantage of the greater illumination. The greater abundance of shade species at the surface in the Mediterranean in winter could be explained by insufficient light for optimum growth of surface species. Under such conditions shade species would develop even though the intensity of illumination were somewhat greater than at greater depths.

TABLE 1. Shade Species of Ceratium. ? indicates either insufficient data or that the results were not conclusive; . . . indicates no record.

Species	Subsurface in summer, Mediterranean	Subsurface Dana collection	Subsurface Carnegie collection
<i>C. praelongum</i>	+	+
<i>C. cephalotum</i>	+	+
<i>C. gravidum</i>	+	+	+
<i>C. digitatum</i>	+	?	+
<i>C. belone</i>	+	—	?
<i>C. incisum</i>	+	—	?
<i>C. subrobustum</i>	—	+
<i>C. Kofoidii</i>	+	—	—
<i>C. setaceum</i>	+	?	?
<i>C. geniculatum</i>	?	?	?
<i>C. Bigelowii</i>	?	?
<i>C. euaucatum</i>	+	+	+
<i>C. filicorne</i>	+	+
<i>C. symmetricum</i>	+	+	+
<i>C. aziale</i>	+	+
<i>C. asoricum</i>	—	?
<i>C. arietinum</i>	+	+	+
<i>C. lunula</i>	+	+	+
<i>C. paradoxides</i>	+	+
<i>C. platycorne</i>	+	+	+
<i>C. ranipes</i>	+	+	+
<i>C. trichoceros</i>	+	—	+
<i>C. vultur</i>	(Pavillardii)	+	+
<i>C. horridum</i>	(molle and claviger)	+
<i>C. tenue</i>	+	+	+
<i>C. arcticum</i>	?
<i>C. longissimum</i>	+	+	+
<i>C. hexacanthum</i>	+	—
<i>C. reflexum</i>	+	+

SUMMARY

1. The distributions of the species of Ceratium of the Carnegie plankton collections from the North Atlantic, North Pacific, and South Pacific were studied in relation to certain environmental conditions.

2. The distributions of Ceratium species do not seem to be affected by the variations in salinity which exist in these oceans.

3. The distributions of most species are so well bounded by temperature lines that a geographic classification of the species was made on the basis of temperature. Only three main categories were recognized: tropical, subpolar, and cosmopolitan. No evidence of temperate species was found.

4. There is a negative correlation between the relative concentration of phosphate in the photic zone and the number of species per station within each large oceanic area but comparisons of large areas show that the number of species does not depend upon the absolute concentration of phosphate present.

5. Currents are probably important in displacing species from their "normal" range, at least temporarily. Certain tropical species are sometimes found in waters of relatively low temperature in currents flowing out of tropical regions.

6. The action of some undetermined chemical substance in limiting the distribution of Ceratium species has yet to be proven.

7. The areas traversed by the Carnegie were divided on the basis of the composition of their Ceratium floras into five regions: Cold North Atlantic, Warm Atlantic, Cold North Pacific, Warm Pacific, and Southeast Pacific. Each region is characterized by particular environmental conditions and by a particular richness of species.

8. The fact that eight species of the collection were found only in the Pacific and no species was confined to the Atlantic tends to indicate that tropical species of the Atlantic find ready access to the Pacific via the Indian Ocean but Pacific species are not carried to the Atlantic because of the current and environmental conditions.

9. The existence of shade species of Ceratium is confirmed. At least 20 of the 58 species studied are probably shade species as they showed an increase in frequency from the surface to 100 meters depth.

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VEGETATION ON THE PEAT LANDS OF DANE COUNTY,
WISCONSIN

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	119
REVIEW OF PREVIOUS WORK.....	119
CLIMATE	120
GEOLOGY	120
DRAINAGE	121
SOILS	121
METHODS	121
NATIVE VEGETATION AT TIME OF SETTLEMENT.....	122
PRIMARY PLANT SUCCESSIONS (PRISERES).....	122
The Bog Sere.....	122
The Hydrosere	123
SECONDARY PLANT SUCCESSIONS (SUBSERES).....	124
Factors Causing Subseres.....	124
Subseres Following the Larix Consocieties.....	124
Undrained Lands	124
Drained Lands	125
Subseres Following the Calamagrostis-Carex Associates	125
Undrained Lands	127
Drained Lands	127
Subseres on Burned Lands.....	132
Superficial Burning	132
Medium Burning	134
Deep Burning	137
Subseres Induced by Soil Disturbances.....	137
SUMMARY	139
LITERATURE CITED	139

VEGETATION ON THE PEAT LANDS OF DANE COUNTY, WISCONSIN¹

INTRODUCTION

Studies of vegetation in relation to peat beds and their formation have always been a fascinating problem to ecologists. The extensive literature deals chiefly with causes and factors involved in development. The papers dealing with plant successions on peat lands usually treat the undisturbed development of vegetation from its initial appearance in the area to the climax or subclimax vegetation. There is comparatively little literature which discusses the plant successions of native vegetation on the peat lands as they are modified by introduced, biotically-controlled factors.

The purpose of this paper is to present the results of studies during 1934 and 1935 on the ecology of the vegetation on the peat lands in the glaciated part of Dane County, Wisconsin, with special reference to such introduced biotically-controlled factors as artificial drainage, cutting and grubbing of trees and shrubs, mowing, grazing, burning, and soil disturbances.

The writer gratefully acknowledges the encouragement and help of Professors L. F. Graber, Aldo Leopold, and B. M. Duggar, University of Wisconsin, during the progress of the work. He also wishes to express his appreciation for the aid extended by Doctor N. C. Fassett, University of Wisconsin, in identifying some of the species of plants, and to Doctor J. H. Robertson, University of Nebraska, for a critical reading of the manuscript.

REVIEW OF PREVIOUS WORK

It is not intended to review all of the voluminous literature which deals with bog successions and the consequent development of peat. Dachnowski (1921) groups bogs into two classes with respect to their method of origin: (1) water-laid peat deposits, that is, the peat developed in depressions occupied by standing water, such as lakes and ponds, and under conditions of poor drainage, and (2) land-laid deposits, that is, the peat deposits accumulated on moist, flat land under conditions of a rising or fluctuating water table. Rhodes (1933) enumerates the various factors concerned in the formation of bogs. He describes two bogs, one ecologically young, the other decidedly older, with respect to plant succession. These two bogs are located in close proximity to Dane County. Dachnowski (1925) found that profiles of peat areas in glacial Lake Wisconsin resemble closely those which he studied in Dane County.

Dachnowski (1921), Soper (1919), and Rhodes (1933), as a result of their microscopic studies of peat profiles, and Auer (1930), Draper (1929), Sears (1932), and others from pollen analysis studies have presented evidence which suggests that marked climatic changes, in addition to the normal succession of plants in bogs, have been instrumental in determining

the nature of the peat beds on the glaciated lands. Sears (1935) has reviewed the literature pertaining to the hypothesis concerning the nature of the climate and of the vegetation during postglacial times.

Dachnowski (1912) estimates that peat developed at the rate of about 1 foot in 2 centuries; Soper and Osbon (1922) place their estimate at 1 or 2 inches per 100 years, while Sears (1932) thinks that about 4 inches accumulate every 100 years.

Weaver and Clements (1938), in their classification of the climax vegetation of North America (frontispiece map), indicate that Dane County lies on the border line between the deciduous forest and the grassland formations. They describe the corresponding associations involved in Wisconsin as the oak-hickory (*Quercus-Carya*) association and the tall-grass prairie (*Andropogon-Sorghastrum*) associates of the true prairie (*Stipa-Sporobolus*) association. This classification refers primarily to the vegetation of the mineral soils, which provide environmental conditions vastly different from those of the peat soils. Recorded evidence is meager as to just what the vegetation was on the peat lands of Dane County at the time of settlement.

Chamberlin (1882), in compiling a geological survey of the state during the period 1873-77, gave some consideration to the types of native vegetation. He recognized 5 types of marsh vegetation, namely, the grass and sedge, the heath, the tamarack, the arbor vitae, and the spruce types. In his general map of the native vegetation prepared in 1882, he shows that the peat lands of Dane County were covered with grass and sedge marsh vegetation; there are no records of shrubs or trees. Owing to the broad generalization given to a discussion of the native vegetation and the very small scale reproduction of his map, detailed accuracy of Chamberlin's classification is not possible. Dachnowski (1925), in describing profiles of peat lands within the limits of extinct lakes Agassiz and Wisconsin, points out that the vegetation present in the vicinity of the profiles when the white man came was reported to have been largely tamarack with heath shrubs and a ground cover of sphagnum. He indicates that the vegetation, in general, on the peat lands of this area included numerous open sedge and reed marshes with no timber, as well as areas forested with tamarack, spruce, and occasionally white pines.

Stallard (1929), in a classical piece of work on secondary successions in the forest formations of northern Minnesota, discusses subseries of bogs. He points out that several factors, namely, damming of natural drainage outlets, drainage ditches, removal

¹ A portion of a thesis submitted to the faculty of the University of Wisconsin in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The work was supported partly by a Research Fellowship in the Graduate School during the academic year 1934-1935.

of trees by cutting and burning, may start subseres in a bog. The secondary successions, complicated by a variety of conditions created by various denuding forces, are discussed under the following heads: (a) subseres in shallow water, (b) subseres beginning with the grass associates, (c) subseres in cut-overs, and (d) subseres in drained, cultivated bogs. Cooper (1913), in writing about the climax forest of Isle Royale, Lake Superior, states that if the bog forests are burned over, the coniferous element is destroyed and the birches, if present, sprout from the stump. Rhodes (1933), in discussing 2 peat bogs in Jefferson County, Wisconsin, cites an illustration of a Larix area which had been cleared of this species for a period of 5 years and had grown almost entirely to *Cornus stolonifera*, *Rhus vernix*, grasses, and sedges. He calls attention to a waste area which has grown to *Salix* spp., *Aster* spp., *Solidago* spp., and others.

Alway (1920) lists the following dangers which may accompany the burning of peat: (1) exposure of underlying poor soil especially if the peat is shallow, (2) lowering of the soil surface which may make the land very wet, (3) increase in alkali, (4) loss of organic matter and nitrogen, and (5) starting serious forest fires. McKibben, Atkinson, and Boone (1936) point out the danger of excessive draining and burning of peat lands.

Stout (1914), in a detailed study of a typical wild-hay marsh meadow on the edge of Madison, Wisconsin, found 110 species in the meadow including 68 forbs, 12 grasses, 22 sedges and rushes, 4 shrubs, and 4 musci. Costello (1936), in making a study of the tussock meadows of southeastern Wisconsin, found that the meadows were dominated by a single species, *Carex stricta*. He concluded that in succession, the tussock association is usually preceded by the reed-swamp stage and followed by the sedge-rush stage. Costello believes that evaporation, annual fires, and soil reaction are not significant factors in succession, but that overgrazing may result in the replacement of the tussock association by grassland. Bergman (1919), in discussing the nature of the primary successions of the swamps of Minnesota, also gives some attention to secondary successions. He classifies them a (1) flooded succession and (2) burn or clearing succession.

The appearance of various bryophytes as pioneers on burned-over lands has been noted by a number of workers, namely, Durand (1908), Humphrey and Weaver (1915), Skuteh (1929), Torrey (1932), Griggs (1933), and Graff (1936).

CLIMATE

The climatic data² should resemble closely those of the entire county.

The mean annual temperature is 46.0° F., with mean monthly temperatures of 17.3° F. for January and 72.5° F. for July. The lowest temperature recorded was -29° F. in January, but there are com-

paratively few days during the winter when the temperature drops below zero. The highest temperature recorded was 107° F. during July but temperatures as high as 100° F. are rare. The average length of the growing season between killing frosts is 174 days, from April 26 to October 17. Freezing temperatures, however, have been recorded during all months.

The average annual precipitation is 31.32 inches, occurring largely during the growing season. Two and one half or more inches of precipitation fall during each month from April to September, inclusive. However, droughts of unusual intensity occurred in 1934 and 1936 and dry periods during July and August are not infrequent. The average seasonal snowfall is 37.7 inches. Annual sunshine is 53 percent of the possible amount, with monthly sunshine ranging from 37 percent for December to 70 percent for July.

The peat soils commonly freeze to depths of 6 to 30 inches after mid-November, and during summer nights cold air settles in these low areas. These factors, coupled with the high moisture content and the low heat conductivity of the peat, result in cold soils during the growing season. However, temperatures of both the air and the soils during the growing season are normally well within the ranges critical for the native plants of the peat lands and are probably of secondary importance.

GEOLOGY

Since the peat lands are confined almost entirely to the glaciated part of the county, only this area will be considered. The rock formations are concealed by glacial drift of a few inches to over 100 feet in depth. Many small exposures, however, do occur. The peat beds are underlain with the following formations: Mendota limestone, Madison sandstone, St. Peter sandstone, and Lower Magnesian limestone. In most instances, these beds are either underlain with or lie adjacent to upland soils which overlie limestone rock.

The work of Pleistocene glaciation and of water courses has been largely responsible for modifying the topography so as to provide environmental conditions favorable for the accumulation of peat beds. Alden (1918) presents in considerable detail the quaternary geology of southeastern Wisconsin. His work indicates that the Illinoian stage and Substage III of the Wisconsin Ice exerted most of the influence on the topography of the glaciated part of Dane County. The Illinoian ice sheet apparently covered more area in the county than any other. This was followed by a considerable period of deglaciation during which the surface of the Illinoian drift was subject to weathering and a soil developed. The Wisconsin stage of glaciation which followed was rather complex. Substage III exerted much influence as it was the last of the glaciers to arrive. When the ice began to melt, interruptions occurred. Stages of halt or readvance and halt caused the development of several marginal moraines, namely, the Johnstown moraine, the Milton moraine, and the Lake Mills moraine system.

² Data from the Annual Meteorological Summary, 1936, of the Madison, Wisconsin Office of the United States Weather Bureau. Madison is located in Dane County.

DRAINAGE

The natural drainage system of the glaciated area is largely the result of glaciation, although the preglacial rock topography exerts some influence. The preglacial valleys were partially or entirely blocked with morainal drift. The drainage system following the disappearance of the glaciers was an imperfect, ineffective system, as compared with preglacial drainage, and it is still in an immature stage of development.

The Yahara River with its tributaries flows southward and southeastward through the glaciated area. The river is interrupted by the four lakes Mendota, Monona, Waubesa, and Kegonsa (Fig. 1). A few tributaries of the Wisconsin and Sugar rivers, which flow through the Driftless Area, extend into the western end of the glaciated area. Waterloo Creek, Koshkonong Creek with its tributary Mud Creek, and another small creek, which empty their waters into the Rock River to the east and south of Dane County, drain the eastern approximate one fourth of the county. In addition to the four large lakes located on the Yahara River, there are other smaller lakes within the county, such as Wingra, Goose, and Mud lakes. A small portion of Lake Koshkonong, also, extends into the county.

TABLE 1. Larger Drainage Projects Established in Dane County.

No.	Name of Project	Township Location	Years	Acres ¹
1	No. 1 Medina.....	Medina.....	1901-05	1,000
2	Badfish-Oregon Branch.....	Oregon, Rutland.....	1906-10	1,000
3	Koshkonong-Mud Creek.....	Deerfield, Christiana.....	1906-10	5,000
4	Nine Springs Creek.....	Fitchburg, Blooming Grove.....	1906-10	1,400
5	Rattlesnake.....	Cottage Grove, Medina, Sun Prairie.....	1906-10	2,525
6	Sheppard.....	York, Bristol, Medina.....	1906-10	4,000
7	Albion.....	Albion.....	1911-15	1,300
8	Rattlesnake Add. No. 1.....	Cottage Grove, Medina, Sun Prairie.....	1911-15	1,500
9	Rutland.....	Rutland.....	1911-15	3,000
10	Starkweather.....	Burke, Blooming Grove.....	1911-15	3,000
11	Blooming Grove.....	Blooming Grove.....	1916-18	2,000
12	Door Creek.....	Cottage Grove.....	1916-18	5,000
13	Clark's Add. to Rattlesnake.....	Cottage Grove.....	1916-18	1,335
14	Lower Badfish.....	Rutland.....	1916-18	5,000
15	No. 2 Westport.....	Westport.....	1919-20	680
16	Marshall.....	York.....	1923-24	3,480
17	No. 9 Sun Prairie.....	Sun Prairie, Burke.....	1923-24	2,520
18	No. 12 Pleasant Springs.....	Pleasant Springs.....	1925-26	1,280
Total Acreage.....				45,020

¹Includes total area involved in project.

It should be recognized that, in general, the natural drainage system is slowly becoming more effective, with the resultant gradual drying of the peat lands, even if unaffected by man.

Eighteen large drainage projects, including a total of approximately 45,000 acres, were completed between 1900 and 1926 (Table 1). Approximately 80

percent (36,000 acres) of this land was wet enough to be affected by artificial drainage. A conservative estimate is that peat lands comprise at least 50 percent of this acreage. Of the approximately 52,000 acres of peat land in the county, at least 40 percent has been artificially drained.

SOILS

The two chief mineral soil types in the glaciated area are Miami silt loam and Carrington silt loam, both derived from glacial limestone till. They consist of 10 to 14 inches of surface soil which is usually acid in reaction and considerably leached. The subsoils are alkaline and heavy. Occasionally, stratified mineral soils are embedded in the outer edges of the peat beds as a result of water erosion. The movement of water through the upland mineral soils into the peat beds has been an important factor in determining soil reactions.

According to Whitson, et al. (1917), there are 52,288 acres of peat soils or 6.8 percent of the total county area (Fig. 1) and 8,448 acres of muck soils, or 1.1 percent of the total area. The peat ranges in depth from about 2 to 20 feet with an average of about 5 feet.

METHODS

Detailed studies were made in Dane County and several inspections were made of the peat lands of other glaciated counties. Although the plant successions are reported primarily for one county they may apply generally to the peat lands of the glaciated part of southern Wisconsin. The seres outlined were determined chiefly by inference. Data and observations which facilitated these deductions involved the composition of the various plant communities, the pioneer and relict species, and so far as possible the history of the areas with respect to the kinds of external influences.

The quadrat method was used for a detailed study of the composition and structure of the vegetation. A modification of Raunkiaer's method, described by Kenoyer (1927) and Hanson and Ball (1928), was employed to the extent that frequency indices and frequency percentages of the species were determined. The composition studies were made during the summer of 1935. All species of Cyperaceae and Juncaceae were placed in one group since it was difficult to identify the species, particularly when quadrats were taken in grazed areas. It was possible with few exceptions to identify all forbs, grasses, trees, and shrubs. The number of plants of each species in each quadrat was also determined, except that the abundance of grasses and of sedges and rushes was indicated only by relative terms, that is, abundant (A), frequent (F), infrequent (I), or scarce (S). Twenty-five quadrats were taken within each plant community. The quadrats, one square meter in size for herbaceous vegetation and nine square meters in size for trees and shrubs, were usually located in a straight line at predetermined intervals of 3 to 5 paces. Where the area was small, the quadrats were arranged in two or more parallel lines.

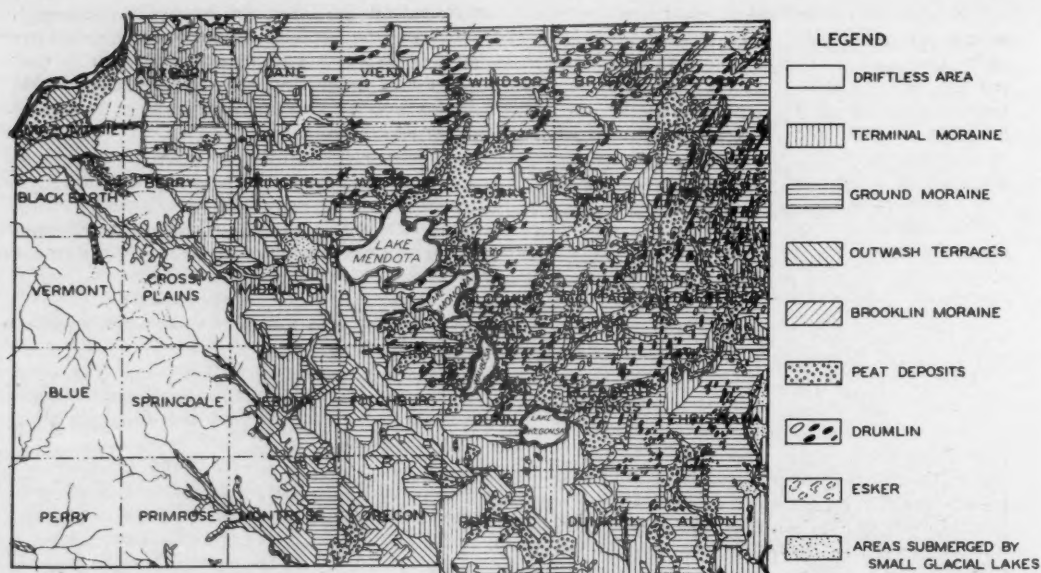


FIG. 1. Surficial deposits of Dane County, Wisconsin. Based on map prepared by William C. Alden of the United States Geological Survey.

NATIVE VEGETATION AT TIME OF SETTLEMENT

Concerning the virgin vegetation of this area, Dachnowski (1921, 1925), and Truman (1933) suggest that a climate of rising temperatures and (or) decreasing precipitation is probably being approached, which is superseding a moist period possibly associated with lower temperatures. The grass and sedge marsh vegetation would probably become the dominant vegetation under conditions of a highly humid, cold climate; whereas, the bog trees and shrubs would gradually replace the herbaceous vegetation with the return of a climate of rising temperatures and decreasing precipitation.

It is difficult to ascertain accurately the relative importance and distribution of the stages of primary succession, either the bog sere or the hydrosere. It appears, however, that much of the peat land had reached the *Larix* stage. This contention is supported by evidence furnished by the presence of relict communities, the presence of *Larix* in undisturbed bogs in adjacent counties, and the statements of pioneer residents. Much of the remainder of the peat lands was covered with sedge and grass vegetation, a condition partially explained by the theory of changing climate. In addition, certain peat lands, particularly those lying within what Chamberlin (1877), has designated as prairie areas, may have been subject to at least occasional prairie fires. This may have prevented invasion by trees and shrubs, and thus maintained a herbaceous cover.

The bog sere does not provide for the sedge grass stage, which normally does not appear under the present climatic conditions where external biotic influences are not at work. It is evident, however, from a study of peat profiles made by other workers that

such a stage did appear for considerable periods during prehistoric time. It may have been interpolated at any stage in the sere following the floating sedge mat stage, whenever the prehistoric climate was not favorable to the development of the tree stages.

PRIMARY PLANT SUCCESSIONS (PRISERES)

THE BOG SERE

Observations of several developing bogs in other counties as well as evidence furnished by the work of Rhodes (1933), Hansen (1933) and others indicate that a bog sere as outlined below may be representative of conditions which prevailed on the peat lands within Dane County in the past.

Bog sere:

1. Submerged stage (*Chara*-*Myriophyllum* associes)
2. Floating stage (*Nymphaea*-*Potamogeton* associes)
3. Floating sedge mat (*Carex* consocies)
4. Sphagnum stage (*Sphagnum* consocies)
5. Bog shrub stage (*Chamaedaphne*-*Andromeda* associes)
6. Coniferous tree stage (*Larix* consocies) (serclimax)
7. Hardwood tree stage (*Populus*-*Salix* associes) (subelimax)

It must be recognized that modifications of this sere undoubtedly occurred as can be inferred from the stages which now appear in existing bog seres of other glaciated counties in southern Wisconsin. It is readily conceivable that any of the above stages might have been omitted, especially as a result of sudden changes in environmental conditions or that other stages might have been interpolated; the former is much more likely.

Peat accumulates chiefly under the bog sere and only to a limited extent under the hydrosere type of plant succession. Although the former was an important sere in the past on the peat lands of Dane County, the present high moisture conditions make the hydrosere much the commoner prisere. Over most of the glaciated part of the county there is sufficient drainage, either natural or artificial, to insure better aeration than that of normal bogs.

This change in the water relation has brought about changes in the composition of the native vegetation. Such species as *Chamaedaphne calyculata*,³ *Andromeda glaucophylla*, *Kalmia polifolia*, *Vaccinium* spp., *Sarracenia purpurea*, *Drosera rotundifolia*, *Eriophorum virginicum*, *Menyanthes trifoliata*, *Sphagnum* spp., and others commonly associated with typical stages of the bog sere, now exist only as relicts (Fig. 2). The occasional relict communities

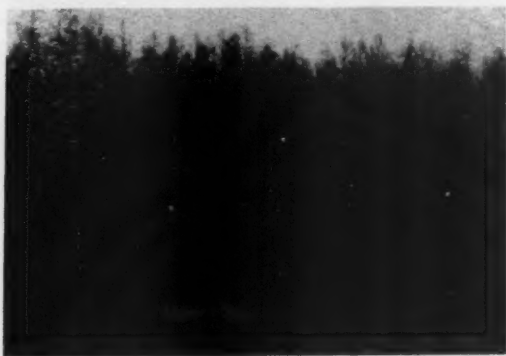


FIG. 2. Vegetation of the bog sere with *Chamaedaphne calyculata* in the foreground and *Larix laricina* in the background. March 23, 1935.

of *Larix* invariably have an understory of *Rhus vernix* and frequently a marginal intermixture of *Betula pumila glandulifera*. The latter is most successful under adverse conditions and with the other woody species tends to survive gradually disappearing herbs. These species are well adapted to grow in the cold, physiologically-dry environment characteristic of bogs, but they do not withstand the competition of other more aggressive, hydrophytic species characteristic of the hydrosere.

Soil tests made by the writer show that most of the peat soils in Dane County, whether artificially drained or not, have a pH value of 6.0 to 7.0 and in no case tested were any of the peat beds lower than pH 6.0, while a pH of 4.5 is common in Wisconsin bogs. These facts furnish additional evidence as to why the typical bog vegetation has largely disappeared.

THE HYDROSERE

With the almost complete disappearance of the bog sere, the hydrosere has become, in spite of artificial drainage, the common type of primary plant succession.

³ Nomenclature is according to the usage of Hitchcock (1935) for grasses, and Gray (1908), with some changes, for other species.

sion around the lakes, ponds, swales, marshes, and along streams. Here a complete, undisturbed hydrosere normally occurs as outlined below. Certain stages may be omitted when rapid changes occur in the controlling environmental factors.

The hydrosere:

1. Submerged stage (*Chara*-*Myriophyllum* associes)
2. Floating stage (*Nymphaea*-*Potamogeton* associes)
3. Reed-swamp stage (*Typha*-*Scirpus* associes)
4. Sedge-meadow stage (*Calamagrostis*-*Carex* associes)
5. Shrub stage (*Salix*-*Cornus* associes)
6. Hardwood-tree stage (*Populus*-*Salix* associes) (subclimax)

It was not within the scope of this work to study the first two stages of the hydrosere.

The reed-swamp stage, in the aggregate, is a large community occupying shallow water and constantly saturated soil. Its zones of dominant species, *Typha latifolia*, *Scirpus validus*, *S. acutus*, *Phragmites communis*, and *Sagittaria latifolia* vary in width from a few feet to one half mile or more. *Typha latifolia*, because of its innumerable, highly mobile seeds, is the most widely distributed. *Scirpus validus* and *S. acutus* usually grow in the deepest water and *Phragmites communis* in the shallowest, although the five dominants are commonly intermixed. *Phragmites communis* often grows in localized patches, whereas the other species have a more general distribution.

There are a number of species of secondary importance in the reed-swamp stage which, in some instances, are abundant in local situations. *Leersia oryzoides* occasionally makes up nearly pure stands within or on the outer border of this zone. *Sagittaria cuneata* commonly occurs in intermixture with the more abundant *S. latifolia*. Others are *Polygonum* spp., *Zizania aquatica*, *Sium suave*, *Allisma plantago-aquatica*, *Lemna* spp., *Penthorum sedoides*, and *Ludwigia palustris*. The last two species are generally confined to the drier limits of the zone.

The sedge-meadow stage follows aggressively the reed-swamp stage on peat land where the water table stands at or a few inches above the surface of the soil during the spring and early summer, but recedes a few inches below the surface during the latter part of the summer. It is characterized by such sod-forming dominants as *Calamagrostis canadensis*, *Carex* spp., and to a lesser degree by *Eleocharis* spp. and *Juncus* spp. with a mixture of other herbs to be considered later.

The sedge-meadow stage is invaded by such shrubby species as *Salix* spp., *Cornus stolonifera*, and *Betula pumila glandulifera*, all dominants of the shrub stage. The several species of *Salix* are the most aggressive and common because of effective propagation by both root sprouts and seeds. *Cornus stolonifera* invades more slowly but once established it propagates freely by rhizomes. As these bushy plants increase, the intolerant sedge-meadow species are shaded out.

As the water level continues to recede, certain trees gain dominance over the shrubs, giving rise to the

Populus-Salix associes. *Populus tremuloides* and several tree species of Salix are the dominant species. *Populus deltoides* comes in but does not tolerate the environment of the peat soils nearly as well as does *P. tremuloides*. *Betula papyrifera*, a common species of peat lands in northern Wisconsin, reaches the limit of its range in Dane County and seldom appears on the peat lands. The shrubby species of the Salix-Cornus associes commonly persist as a lower stratum and in the openings.

At present, no conclusion can be drawn regarding the rate at which the subclimax, Populus-Salix associes, will give way to the climax Quercus-Carya community now on adjacent upland mineral soils. It does appear likely that the immature peat and muck soils will eventually become so dried, decomposed, and packed that they will support the climax vegetation. One instance was noted in which *Quercus velutina* and *Q. macrocarpa* were invading a Larix consocieties on peat. The soil profile consisted of the characteristic layers of sand, clay, marl, and peat ranging in depth from a few centimeters to 3 meters. The average age of 10 of the older specimens of *Larix laricina* was 59 years and that of 10 older *Quercus velutina* trees was 19 years. It is thought that the climax vegetation will eventually dominate this area.

SECONDARY PLANT SUCCESSIONS (SUBSERES)

FACTORS CAUSING SUBSERES

A brief consideration will be given to the methods by which man has controlled the secondary successions. The drier soil resulting from lower water tables following drainage has not only brought about distinct changes in the types of vegetation but has also led to intensification of such factors as burning, grazing, and mowing. The land in the immediate vicinity of ditches is more effectively drained than that some distance away. This differential efficiency in drainage brings about zonation in the vegetation on the various parts of a drained area, the more advanced stages lying in closer proximity to the ditches.

Since pioneer days, cutting and grubbing of Larix trees have continued so intensively that only small areas of the once extensive forests remain. In some instances others, such as *Populus tremuloides*, *P. deltoides*, and *Salix* spp. have appeared and these have been removed by cutting, grubbing, or both. Much of the peat land is devoted to grazing, while other areas supporting desirable herbaceous vegetation serve as a source of hay. The repeated annual mowing must be recognized as an ecological factor; for example, ecesis of shrubs and trees is prevented in such areas. Burning plays a role in plant succession which varies with its frequency and intensity from an occasional superficial fire to burns penetrating to the underlying substratum. Several kinds of soil disturbances, usually local, have influenced the vegetation. These include disturbances created by drainage ditches, ditch banks, trampling by livestock, and removal of peat for fuel; only the last is unimportant.

SUBSERES FOLLOWING THE LARIX CONSOCIETIES

Evidence has been presented that two principal types of vegetation originally may have occupied many of the peat lands of Dane County. These two types are the Larix consocieties and the Calamagrostis-Carex associes (Fig. 3). The Larix serclimax vegeta-



Fig. 3. Calamagrostis-Carex associes (partially mowed) in the foreground and Larix consocieties in the background. July 20, 1935.

tion, if undisturbed by external, biotic influences will persist until replaced by the Populus-Salix associes, a subclimax unit.

Undrained Lands

The type of subseres initiated by the cutting of Larix appears to be determined by the nature of subsequent treatment. It is inferred from a study of present vegetation that a definite succession of communities has occurred and may be regarded as normal.

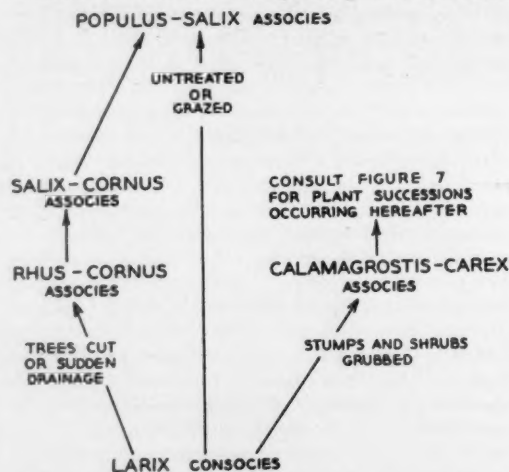


Fig. 4. The types of plant successions following the Larix consocieties stage as influenced by various treatments. The resulting plant successions are similar whether or not the land is artificially drained except that succession takes place much more rapidly on drained lands.

Where only *Larix* is removed, the lower story of *Rhus vernix* shrubs becomes dominant. *Cornus stolonifera*, usually present as scattered plants, increases and, accordingly, a unit of vegetation develops which is recognized as the *Rhus-Cornus* associes. This stage is gradually replaced by the *Salix-Cornus* associes and eventually by the *Populus-Salix subelimax* (Fig. 4). The *Rhus-Cornus* associes and the *Salix-Cornus* associes are usually characterized by a number of subdominant species, namely, *Betula pumila glandulifera*, *Impatiens biflora*, *Muhlenbergia foliosa*, *Solidago* spp., *Eupatorium maculatum*, and *Eupatorium perfoliatum*.

If the tree stumps and the shrubs are grubbed, the land usually is utilized for hay. The succeeding community, necessarily herbaceous, is usually the *Calamagrostis-Carex* associes.

Drained Lands

If the land is artificially drained, the *Larix* community suffers severely in the drier environment (Fig. 5). While this factor has exerted its influence for



FIG. 5. An artificially-drained area in which the *Larix laricina* trees have been killed by the dry environment of the soil and other factors. July 20, 1935.

many years, it is greatly accentuated during dry years such as 1934. The older trees of *Larix* have a shallow, horizontal root system which originally grew and developed above a high water table. Emerson (1921) has shown that the roots of *Larix laricina* will not grow vertically into water but in a horizontal position above it.

This was verified by the writer in a study of the root systems of trees uprooted by wind. Most of the roots were confined to the upper 2 feet of soil (Fig. 6). Artificial drainage has, in most instances, lowered the water level to such depths that most of the roots of the trees are left in a drained layer of soil. The root systems are suddenly exposed to a soil which becomes at least periodically dry. Although *Larix* grows best on aerated soils, those trees whose root systems developed in extremely wet soils cannot become readily readjusted to much drier soils. In a



FIG. 6. A *Larix laricina* tree uprooted by wind. Note the shallow, lateral type of root system. March 23, 1935.

few communities there are young trees which began growth since drainage of the peat beds. These younger trees develop a deeper, more nearly vertical root system and are able to cope more effectively with the adverse factors.

A direct biotic factor which has injured *Larix* is the larch sawfly, a serious leaf-eating pest in Wisconsin. The weakened trees are more susceptible to destruction by such other insects as the bark beetles. The most severe infestations have occurred in the northern part of the state but severe infestations have occurred as far south as Dane County.⁴ Destruction is worse during dry years because parasites of the sawfly larvae tend to hold them in check during moister periods.

As natural drainage gradually becomes more effective, the *Larix* consocies is normally replaced by the *Populus-Salix* associes (Fig. 4). However, after artificial drainage *Larix* sometimes dies more rapidly than *Populus* and *Salix* can replace it. As a result, the *Rhus-Cornus* associes and the *Salix-Cornus* associes often become intermediate stages in the succession.

On drained peat land successions initiated by grazing and by cutting and grubbing of *Larix* are similar to those on undrained lands, but progress more rapidly.

SUBSERES FOLLOWING THE CALAMAGROSTIS-CAREX ASSOCIES

The aggregate area of the *Calamagrostis-Carex* associes vegetation has been greatly increased by the destruction of the *Larix* consocies, the former having replaced much of the latter. However, many peat lands, long occupied by the *Calamagrostis-Carex* associes, are at present occupied by other stages of succession.

Composition studies were made of three plant communities of the *Calamagrostis-Carex* associes of the hydrosere succession. Tables 2 and 3 present the composition and frequency of species in two different parts of a comparatively recently-developed belt of

⁴ Personal communication from E. L. Chambers, State Entomologist of Wisconsin.

vegetation around a small, receding lake. The recent origin of this community was indicated by the presence of relict *Typha* and *Scirpus* scattered through it together with a *Typha-Scirpus* zone along its wetter border. The data in Table 2 were obtained in the outer border of the zone, that is, in the older part, while those in Table 3 were obtained on the inner, more recently developed part of the zone. The data in Table 4 were obtained in a hay meadow in which a *Larix* community had been replaced by *Calamagrostis-Carex* type of vegetation after the trees of the former had been removed by grubbing. An attempt had been made to drain this area artificially, but the shallow ditch had been partially filled.

An analysis of the data of Tables 2, 3, and 4 shows the prominence and the importance of *Calamagrostis canadensis* and the several species of sedges and rushes. All of them appeared in every quadrat of the three series. Grasses of secondary importance in this associates are *Poa pratensis*, *Agrostis alba*, *Agrostis hiemalis*, *Muhlenbergia racemosa*, *M. foliosa*, *Sphenopholis obtusata*, *Calamagrostis inexpectata*, *Poa palustris*, *Glyceria canadensis*, and *Phalaris arundinacea*. *Poa pratensis* and *Agrostis alba* are aggressive invaders and are especially likely to appear when grazing occurs. *Agrostis hiemalis* sometimes develops local, dense stands. *Muhlenbergia foliosa* is quite aggressive and although seldom abundant it is generally distributed. The other species are neither particularly aggressive nor common.

Forbs commonly found in this associates are *Dryopteris thelypteris*, *Lycopus uniflorus*, *L. americanus*, *Hypericum virginicum*, *H. majus*, *Galium* spp., *Lysimachia thyrsiflora*, *Mentha arvensis canadensis*, *Polygonum amphibium*, *harterrightii*, *Bidens trichosperma*, *Campanula aparinoides*, and *Viola* spp.

TABLE 2. Composition and Frequency of Species in a *Calamagrostis-Carex* Associates Developed on a Recently-exposed Lake Bed, near Oregon, July 15, 1935.

	Number of quadrats in which each species was found		Total number of individual plants ¹
	Total	Percent	
<i>Calamagrostis canadensis</i>	25	100	A
Sedges and rushes.....	25	100	A
<i>Lycopus uniflorus</i>	25	100	532
<i>Lycopus americanus</i>	25	100	182
<i>Hypericum virginicum</i>	12	48	39
<i>Hypericum majus</i>	10	40	32
<i>Polygonum coccineum terrestre</i>	7	28	12
<i>Polygonum amphibium</i> <i>harterrightii</i>	5	20	9
<i>Cirium lanceolatum</i>	3	12	3
<i>Stachys palustris</i>	2	8	5
<i>Potentilla norvegica hirsuta</i>	2	8	2
<i>Muhlenbergia</i> spp.	2	8	1
<i>Galium claytoni</i>	1	4	3
<i>Glyceria canadensis</i>	1	4	1
<i>Eupatorium perfoliatum</i>	1	4	1
<i>Scirpus validus</i>	1	4	1
<i>Poa pratensis</i>	1	4	S

¹In this and following tables the frequency of the species of grasses and of the sedges and rush group is expressed by the following terms: A - abundant (individuals numerous on the quadrats in which they occur); F - frequent (a sprinkling of individuals); I - infrequent; S - scarce.

TABLE 3. Composition and Frequency of Species in a *Calamagrostis-Carex* Associates Developed on a Recently-exposed Lake Bed, near Oregon, July 16, 1935. This Plant Community is of More Recent Origin than that Presented in Table 2.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Calamagrostis canadensis</i>	25	100	A
Sedges and rushes ¹	25	100	A
<i>Hypericum virginicum</i>	25	100	374
<i>Lycopus uniflorus</i>	25	100	341
<i>Lysimachia thyrsiflora</i>	16	64	70
<i>Scirpus validus</i>	16	64	S
<i>Lycopus americanus</i>	13	52	36
<i>Polygonum amphibium</i> <i>harterrightii</i>	7	28	23
<i>Sagittaria latifolia</i>	3	12	4
<i>Hypericum majus</i>	2	8	2
<i>Dryopteris thelypteris</i>	1	4	6
<i>Potentilla palustris</i>	1	4	1
<i>Typha latifolia</i>	1	4	1

¹Except *Scirpus validus*.

TABLE 4. Composition and Frequency of Species in a Hay Meadow, in a *Calamagrostis-Carex* Associates, near Deerfield, July 15, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Calamagrostis canadensis</i>	25	100	A
Sedges and rushes.....	25	100	A
<i>Dryopteris thelypteris</i>	25	100	A
<i>Poa pratensis</i>	18	72	I
<i>Lysimachia thyrsiflora</i>	15	60	62
<i>Solidago serotina</i>	13	52	71
<i>Sphenopholis obtusata</i>	12	48	I
<i>Viola</i> spp.	10	40	46
<i>Bidens trichosperma</i>	8	32	32
<i>Rumex crispus</i>	8	32	11
<i>Lycopus uniflorus</i>	7	28	17
<i>Agrostis hiemalis</i>	6	24	I
<i>Mentha arvensis canadensis</i>	5	20	39
<i>Cirium muticum</i>	5	20	35
<i>Stellaria longifolia</i>	5	20	18
<i>Aster junceus</i>	5	20	9
<i>Salix petiolaris</i>	4	16	6
<i>Stachys palustris</i>	3	12	5
<i>Campanula aparinoides</i>	2	8	9
<i>Aster puniceus</i>	2	8	3
<i>Agrostis alba</i>	2	8	I
<i>Potentilla palustris</i>	2	8	3
<i>Asclepias incarnata</i>	2	8	2
<i>Sphenopholis obtusata</i>	2	8	I
<i>Potentilla norvegica hirsuta</i>	1	4	6
<i>Scutellaria epilobifolia</i>	1	4	3
<i>Poa palustris</i>	1	4	F
<i>Galium labradoricum</i>	1	4	2
<i>Hypericum majus</i>	1	4	1
<i>Typha latifolia</i>	1	4	1
<i>Eupatorium maculatum</i>	1	4	1
<i>Sagittaria latifolia</i>	1	4	1
<i>Caltha palustris</i>	1	4	1
<i>Salix pedicularis</i>	1	4	1
<i>Trifolium pratense</i>	1	4	1
<i>Muhlenbergia foliosa</i>	1	4	S

Aster, *Solidago*, and *Eupatorium* each contribute aggressive species which, however, achieve their greatest importance on drained land. Of less importance

are *Asclepias incarnata*, *Scutellaria galericulata*, *Caltha palustris*, *Cirsium muticum*, *Lathyrus palustris*, and others.

Undrained Lands

Effect of Mowing—If the Calamagrostis-Carex type is mowed at least every 2 or 3 years, it tends to persist. This stage is usually replaced by other developmental herbaceous stages as the natural drainage system becomes more effective, an aspect discussed more fully under the heading of drained lands. If mowing of the Calamagrostis-Carex type is discontinued, it is rapidly replaced by the Salix-Cornus associates stage and plant succession continues through the normal hydrosere (Fig. 7).

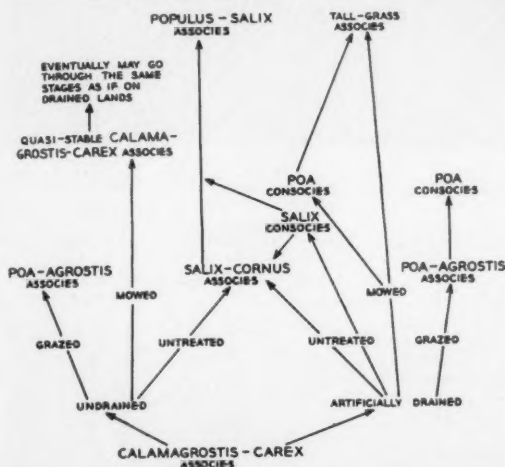


FIG. 7. The types of plant successions following the Calamagrostis-Carex associates stage as influenced by artificial drainage compared with no drainage and correlated with other types of treatment.

Effect of Grazing—Grazing results in some modification of the vegetation. The degree to which the rate of change is hastened by grazing depends upon its intensity and upon the depth of the water level, which fluctuates throughout the year. It is usually at or above the surface of the peat during the spring and early summer months so that the livestock find it extremely difficult to walk over this soft ground and, accordingly, graze the vegetation sparingly. This light grazing permits luxuriant early growth in the Calamagrostis-Carex community. Thus, regardless of the intensity of mid- and late-season grazing, dominants escape severe injury because of accumulated food reserves and reduced palatability accompanying maturity.

As the natural drainage becomes more effective and the soil more compact as a result of livestock tramping, the characteristic species of the Calamagrostis-Carex associates are gradually replaced by the Poa-Agrostis associates, a comparatively stable stage under grazing conditions (Figs. 7 and 8).

If the Calamagrostis-Carex or the Poa-Agrostis grazed lands are neither mowed nor burned, the area



FIG. 8. A pasture consisting of Poa-Agrostis associates. July 20, 1935.

will be taken over by the Salix-Cornus associates stage. Accordingly, occasional use is made of burning when the ground is frozen or the water table is high, in order to prevent the establishment of shrubs. Burning of the dried vegetation during the winter and early spring months, when the ground is frozen and (or) when the water level is high, that is, at or very near the surface, is an effective practice in maintaining a Calamagrostis-Carex or Poa-Agrostis plant community.

Occasionally grazing is of such intensity, particularly in the Poa-Agrostis type, that aftermath is insufficient to support an intense fire and attempts at burning fail to halt invasion by the Salix-Cornus associates. Unless grazing is reduced at 3- to 4-year intervals, the more difficult practices of cutting and grubbing are required.

Drained Lands

The kind of vegetation which eventually replaces the Calamagrostis-Carex type on artificially-drained land is determined by its use. If such areas are undisturbed by external factors such as grazing, mowing, or burning, the vegetation is invaded by the

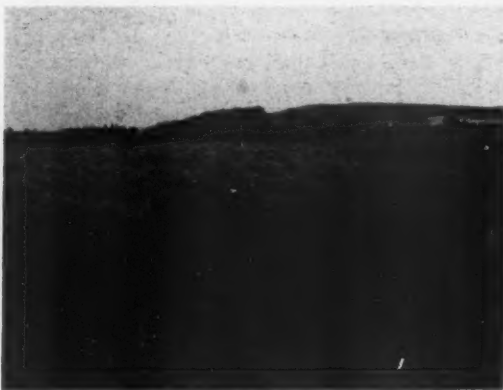


FIG. 9. An artificially-drained pasture invaded by the Salix-Cornus associates. The shrubs are largely *Salix* spp. July 20, 1935.

Salix-Cornus associates (Fig. 9) and eventually by the *Populus-Salix subelimax*. Most of the peat lands supporting the *Calamagrostis-Carex* vegetation are devoted to production of pasturage or hay.

Effect of Mowing—The type of vegetation that replaces the *Calamagrostis-Carex* stage under mowing depends to a considerable extent upon the efficiency of the drainage system. If the peat lands are drained thoroughly, the dominants, weakened by the drier environment, are rapidly replaced by other aggressive, less hydric species, such as *Poa pratensis* and to a limited extent *P. compressa*, giving rise to the *Poa* consociates (Fig. 10).



FIG. 10. A *Poa* consociates hay meadow on artificially-drained land. Note the *Urtica procera* on the drainage ditch in background. July 20, 1935.

Table 5 illustrates the typical composition of a *Poa* consociates on land which, prior to drainage, had been occupied by the *Calamagrostis-Carex* vegetation. Evidence in support of this latter contention is that *Calamagrostis canadensis* and several carices are still presents as relicts, the former species appearing as "scarce" in 15, and the sedge and rush group appearing as "infrequent" in 13 of the 25 quadrats. *Poa pratensis* has been so aggressive, in this instance, that it is obviously the sole dominant.

It is thought that the *Poa* consociates will be eventually replaced by other developmental stages of vegetation. Several examples were noted of the invasion of peat land by *Spartina pectinata* and *Andropogon furcatus* either separately or together. These tall grasses thus become the dominants in an associates, or alone, in consociates.

Certain weedy forbs sometimes appear abundantly on those areas where the *Calamagrostis-Carex* vegetation is gradually disappearing. Apparently these aggressive forbs are taking advantage of the reduced competition existing before a new stage of vegetation takes possession. The more common weedy forbs are *Solidago* spp., *Aster* spp., *Eupatorium* spp., *Urtica procera*, *Potentilla norvegica hirsuta*, and *Helianthus giganteus*. Most of these species are characterized by conspicuity out of proportion to their abundance.

If an area occupied by the *Calamagrostis-Carex* associates is not thoroughly drained, this unit of vegetation is quite persistent but some changes in composition occur among the subdominant species. This associates is eventually replaced by the tall-grass associates (Fig. 7) or by one of the consociates such as *Spartina* or *Andropogon* (Figs. 11 and 12). The tall-grass associates appears to be a disclimax which will persist as long as mowing is continued.



FIG. 11. *Spartina* consociates. *Spartina pectinata* is the dominant species. July 20, 1935.



FIG. 12. A close view of the vegetation in Fig. 11. July 20, 1935.

TABLE 5. Composition and Frequency of Species in a Drained *Poa* Consociates Meadow, near Deerfield, July 13, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Poa pratensis</i>	25	100	A
<i>Calamagrostis canadensis</i>	15	60	8
Sedges and rushes.....	13	52	I
<i>Potentilla norvegica hirsuta</i>	13	52	76
<i>Acrida tuberculata</i>	3	12	6
<i>Polygonum amphibium</i> <i>hasturrightii</i>	3	12	4
<i>Polygonum hydropiper</i>	1	4	2
<i>Dryopteris thelypteris</i>	1	4	2
<i>Urtica procera</i>	1	4	2
<i>Viola cucullata</i>	1	4	1
<i>Salix petiolaris</i>	1	4	1
<i>Rumex crispus</i>	1	4	1

Table 6 presents the composition of the vegetation in a *Spartina* consocieties stage. In this instance, a *Calamagrostis*-*Carex* unit of vegetation on an artificially-drained area has been gradually replaced by the *Spartina* consocieties type. *Spartina pectinata* was the sole dominant with *Dryopteris thelypteris*, a subdominant species, forming an understory. The latter species and a number of others such as *Galium* spp., *Lathyrus palustris*, *Caltha palustris*, *Calamagrostis canadensis*, are relicts of the *Carex*-*Calamagrostis* type. This area, according to local residents, has been burned over a number of times since it was artificially drained. Superficial burning is more detrimental to the shallow-rooted species such as *Poa pratensis*, *Calamagrostis canadensis*, sedges, and rushes, than to *Spartina*, because of its more deeply embedded rhizomes. Certain forbs of this area (Table 6) also tend to increase under burning, for example, *Solidago* spp., *Aster* spp., *Eupatorium maculatum*, and *Urtica procera*.

Table 7 presents the composition of a drained *Calamagrostis*-*Carex* community being invaded by the *Andropogon* consocieties type. *Andropogon furcatus* was abundant in each of the 25 quadrats with the sedge and rush species still playing a very important role. *Calamagrostis canadensis* was absent but *C. inexplensa* appeared in 20 percent of the quadrats. Many of the forbs were those characteristic of the *Calamagrostis*-*Carex* type. Although they were decreasing in numbers, they still constituted a relatively important group. Some forbs, which had appeared with the *Andropogon* consocieties and are to be recognized as normal components of it, are *Phlox pilosa*, *Liatris pycnostachya*, *Hypoxis hirsuta*, *Eupatorium maculatum*, *Solidago* spp., and *Aster* spp.

Weaver and Clements (1938), consider that the tall-grass communities are preclimax to forest and may also serve as a subclimax in its development. The tall-grass associations may be expected to increase its present small holdings on those peat lands which are thoroughly drained, unburned, and mowed regularly.

Effect of Grazing—Grazing of the *Calamagrostis*-*Carex* type usually occupies a longer season and is more severe on artificially-drained than undrained peat lands. The dry environment created by artificial drainage and the generally close grazing and compaction of the soil by the livestock are unfavorable to the species of the *Calamagrostis*-*Carex* type and favorable to other species. The changed environment is particularly well adapted to several exotic species which have been generally disseminated over the upland pastures. The important species are *Poa pratensis*, *Agrostis alba*, and *Trifolium repens*. This unit of vegetation is recognized as the *Poa*-*Agrostis* associations (Fig. 13).

Overgrazing of this type favors the dominance of weedy forbs. Under continued judicious grazing, coupled with occasional mowing, burning, cutting, or grubbing, the type is maintained indefinitely unless the soil becomes too dry for *Agrostis*, in which case, a *Poa* consocieties appears (Fig. 7).



FIG. 13. A ditch bank covered with *Poa*-*Agrostis* associations. July 20, 1935.

Two typical *Poa*-*Agrostis* pastures were sampled. The 2 dominants, *Poa pratensis* and *Agrostis alba* appeared as "abundant" in each of the 25 quadrats of both series (Tables 8 and 9). *Calamagrostis canadensis*, a dominant of the preceding stage, does not withstand heavy grazing nor the drier soils and had disappeared completely. A number of species of sedges and rushes, particularly those which are

TABLE 6. Composition and Frequency of Species in a *Spartina* Consocieties Stage of Vegetation on Drained Land, near Deerfield, July 8, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Spartina pectinata</i>	25	100	A
<i>Dryopteris thelypteris</i>	24	96	327
<i>Solidago</i> spp.....	21	84	264
<i>Thalictrum dasycarpum</i>	18	72	137
<i>Muhlenbergia foliosa</i> ¹	16	64	8
<i>Eupatorium maculatum</i>	13	52	110
<i>Galium</i> sp.....	12	48	87
<i>Lathyrus palustris</i>	9	36	11
Sedges and rushes.....	8	32	8
<i>Aster puniceus</i>	7	28	27
<i>Cirsium</i> sp.....	7	28	8
<i>Stachys palustris</i>	4	16	6
<i>Polygonatum pubescens</i>	4	16	4
<i>Smilacina stellata</i>	3	12	12
<i>Betula pumila glandulifera</i>	3	12	10
<i>Zizia aurea</i>	3	12	7
<i>Urtica procera</i>	3	12	5
<i>Caltha palustris</i>	3	12	3
<i>Poa pratensis</i>	3	12	1
<i>Calamagrostis canadensis</i>	2	8	8
<i>Heliopsis scabra</i>	1	4	3
<i>Aster umbellatus</i>	1	4	4
<i>Ambrosia artemisiifolia</i>	1	4	2
<i>Apocynum cannabinum</i>	1	4	1
<i>Salix discolor</i>	1	4	1
<i>Populus tremuloides</i>	1	4	1
<i>Sisymbrium altissimum</i>	1	4	1
<i>Hypericum majus</i>	1	4	1
Unidentified forb.....	1	4	2

¹ May include some plants of *M. racemosa*.

TABLE 7. Composition and Frequency of Species in a Drained Calamagrostis-Carex Associates Meadow Being Invaded by the Andropogon Consociates type, near Cottage Grove, July 29, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Andropogon furcatus</i>	25	100	A
Sedges and rushes ¹	25	100	A
<i>Parnassia caroliniana</i>	25	100	358
<i>Steironema quadriflorum</i>	25	100	255
<i>Solidago</i> spp.....	25	100	242
<i>Lycopus uniflorus</i>	23	92	284
<i>Viola</i> spp.....	20	80	81
<i>Phlox pilosa</i>	18	72	186
<i>Muhlenbergia racemosa</i> ²	18	72	I
<i>Cirsium muticum</i>	15	60	38
<i>Eupatorium maculatum</i>	15	60	21
<i>Liatris pycnostachya</i>	14	56	39
<i>Sium suave</i>	10	40	17
<i>Aster junceus</i>	9	36	66
<i>Sphenopholis obtusata</i>	7	28	S
<i>Lycopus americanus</i>	6	24	22
<i>Pedicularis lanceolata</i>	6	24	15
<i>Poa pratensis</i>	5	20	I
<i>Calamagrostis inexpectans</i>	5	20	S
<i>Agrostis alba</i>	4	16	F
<i>Hypoxis hirsuta</i>	4	16	I
<i>Salix petiolaris</i>	3	12	6
<i>Liparis loeselii</i>	3	12	6
<i>Rhynchospora capillacea</i>	3	12	I
<i>Salix discolor</i>	3	12	4
<i>Eupatorium perfoliatum</i>	2	8	3
<i>Glyceria striata</i>	2	8	I
<i>Lythrum alatum</i>	1	4	10
<i>Betula pumila glandulifera</i>	1	4	2
<i>Salix bebbiana</i>	1	4	I
<i>Galium labradoricum</i>	1	4	I
<i>Aster puniceus</i>	1	4	I
<i>Eriogon pulchellus</i>	1	4	I
<i>Campanula sparinoides</i>	1	4	I

¹Except *Rhynchospora capillacea*.²Includes a little *Muhlenbergia foliosa*.

low-growing relicts of the preceding stage, had persisted and still played an important role as component species.

The other species in the two areas are of two kinds, namely, relicts of the Calamagrostis-Carex associates and subdominants of the Poa-Agrostis associates. The data in Table 8 were obtained from a younger community than those in Table 9. Most of the species of the younger community are relicts of the immediately preceding Calamagrostis-Carex associates. Examples are *Lycopus uniflorus*, *Viola* spp., *Mentha arvensis canadensis*, *Lobelia syphilitica*, *Glyceria striata*, and *Pedicularis lanceolata*. The older community has fewer relicts, but there are many species characteristic of the Poa-Agrostis associates. Examples are *Verbena hastata*, *Potentilla norvegica hirsuta*, *Polygonum aviculare*, *Acnida tuberculata*, *Taraxacum officinale*, *Ambrosia artemisiifolia*, and *Plantago major*. *Trifolium repens* appears quite generally but is only occasionally abundant locally. *Phleum pratense* is also of some importance. In addition to the forbs previously enumerated as being associated with this associates, several others, namely, *Cirsium lanceolatum*, *Urtica procera*, *Polygonum* spp., *Eupatorium*

TABLE 8. Composition and Frequency of Species in a Poa-Agrostis Associates Pasture, near Cottage Grove, July 6, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Poa pratensis</i>	25	100	A
<i>Agrostis alba</i>	25	100	A
Sedges and rushes.....	25	100	F
<i>Lycopus uniflorus</i>	24	96	229
<i>Viola</i> spp.....	23	92	133
<i>Eupatorium maculatum</i>	14	56	39
<i>Mentha arvensis canadensis</i>	13	52	77
<i>Steironema quadriflorum</i>	13	52	34
<i>Pedicularis lanceolata</i>	9	36	25
<i>Betula pumila glandulifera</i>	9	36	19
<i>Scutellaria epilobifolia</i>	4	16	11
<i>Verbena hastata</i>	4	16	7
<i>Cirsium lanceolatum</i>	3	12	5
<i>Salix petiolaris</i>	3	12	4
<i>Lobelia syphilitica</i>	2	8	9
<i>Equisetum arvense</i>	1	4	1
<i>Taraxacum officinale</i>	1	4	1
<i>Glyceria striata</i>	1	4	S
<i>Trifolium repens</i>	1	4	S

TABLE 9. Composition and Frequency of Species in a Poa-Agrostis Associates Pasture, near Madison, July 18, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Poa pratensis</i>	25	100	A
<i>Agrostis alba</i>	25	100	A
Sedges and rushes.....	16	64	I
<i>Polygonum punctatum</i> and <i>P. hydropiper</i>	11	44	18
<i>Verbena hastata</i>	8	32	18
<i>Potentilla norvegica hirsuta</i>	6	24	10
<i>Trifolium repens</i>	5	20	I
<i>Melilotus</i> sp.....	4	16	13
<i>Polygonum aviculare</i>	4	16	7
<i>Phleum pratense</i>	4	16	S
<i>Acnida tuberculata</i>	3	12	9
<i>Polygonum amphibium</i> <i>hartwegii</i>	3	12	3
<i>Eupatorium maculatum</i>	3	12	3
<i>Taraxacum officinale</i>	2	8	4
<i>Ambrosia artemisiifolia</i>	2	8	4
<i>Plantago major</i>	2	8	4
<i>Pilea pumila</i>	2	8	3
<i>Epilobium coloratum</i>	2	8	2
<i>Rorippa hirsuta glabrata</i>	2	8	2
<i>Viola</i> spp.....	2	8	2
<i>Lycopus uniflorus</i>	1	4	2
<i>Trifolium pratense</i>	1	4	1
<i>Hordeum jubatum</i>	1	4	1
<i>Rumex crispus</i>	1	4	1
<i>Eupatorium perfoliatum</i>	1	4	1
<i>Polygonum persicaria</i>	1	4	1

spp., and *Cannabis sativa* are also characteristic species.

Verbena hastata and *Cirsium lanceolatum* are the two most generally distributed weedy forbs on those peat lands occupied by the Poa-Agrostis associates. They are particularly objectionable because of their abundance and their competition with valuable pasture plants. These weeds are abundant in the transi-



FIG. 14. An artificially-drained, judiciously-grazed pasture of *Poa-Agrostis* associates in foreground; a closely-grazed pasture heavily invaded by *Urtica procera* in background. July 20, 1935.

tion zone between the *Calamagrostis-Carex* and the *Poa-Agrostis* associates. In such environments the water level is below the surface of the soil, yet the soil is sufficiently wet so that grazing livestock break the soil surface considerably and these weeds are provided with a favorable habitat for ecesis. There are numerous examples of zones of *Cirsium lanceolatum*, and fewer of *Verbena hastata*, appearing on the outer margins of the *Calamagrostis-Carex* areas.

Urtica procera is a common weedy forb of narrower distribution but of greater local abundance than *Cirsium* and *Verbena*. *Urtica* has become such a common, highly undesirable weed on the peat lands that its autecology deserves consideration. Its ecological relationships with respect to management practices indicate proper control measures. *Urtica* flourishes on moist, fertile, organic soils; the drained peat provides an especially favorable environment if competition from other species is not too severe. *Urtica* seeds abundantly and is generally distributed

along drainage ditches, fence rows, and other similar places, which then serve as sources for the invasion of other lands such as the *Poa-Agrostis* plant communities (Figs. 14 and 15).

The rate of spread of *Urtica* into the *Poa-Agrostis* community depends upon three important factors, namely, whether burning is practiced, the efforts taken to prevent its spread, and the intensity of grazing. If annual, or even less frequent, burning of the grazed *Poa-Agrostis* lands is practiced, *Urtica* is favored at the expense of the dominant grasses, and consequently, may spread rapidly. *Poa-Agrostis* pastures are usually not burned except to eradicate invading shrubs. However, if *Urtica* begins to appear, burning during the winter months may be resorted to in order to remove its unsightly top growth. Unfortunately, the shallow rhizomes of grasses suffer considerably more than the deeper ones of *Urtica*. The latter is thus favored by reduced competition and its spread is accelerated.

A study of the competition between *Urtica* and the undisturbed dominants of the *Poa-Agrostis* associates is of interest. *Poa pratensis* is a more aggressive species than *Agrostis alba*; consequently the former will be discussed in its competitive relationship with *Urtica*. It was difficult to ascertain accurately whether *Urtica* can invade ungrazed, unburned *Poa pratensis* communities. Fragmentary evidence indicates that this may happen. While it is almost impossible for *Urtica* seedlings to ecesis in a well-developed sod of *Poa*, the former undermine the sod vegetatively by rhizomes 10 to 15 inches below the surface. *Urtica* resumes vigorous growth early so that the effects of its competitive shading come into play early in the season. It bears heavy foliage and grows in dense stands, thus casting deep shade so that other species sparingly invade dense stands of *Urtica*. In addition, by shedding its lower leaves, *Urtica* partially covers lower plants with debris. Consequently, the low-growing *Poa*, in spite of its well-known tolerance, is shaded out. The litter of leaves doubtless hinders the establishment of *Poa* seedlings during the fall months even after *Urtica* is no longer providing competition by shading.

There is a positive correlation between the intensity of grazing of *Poa-Agrostis* associates or *Poa* consocieties pastures and the rate of spread of *Urtica*, once it makes a successful initial invasion. *Urtica* usually invades and occupies local areas which are consequently avoided by the grazing animals. Accordingly, the decreasing acreage of uninfested pasture land is grazed more and more intensively with the result that *Urtica* spreads more rapidly, a constantly accelerating process.

The data in Table 10 show the composition of the vegetation in a *Poa* consocieties pasture heavily invaded by *Urtica procera*. The latter species appeared in 96 percent of the quadrats with an average of nearly 26 plants per square meter. The *Poa* plants, although still abundant in a majority of the quadrats, made a much less desirable sod than that in an adjoining pasture nearly free of *Urtica*. There are conditions

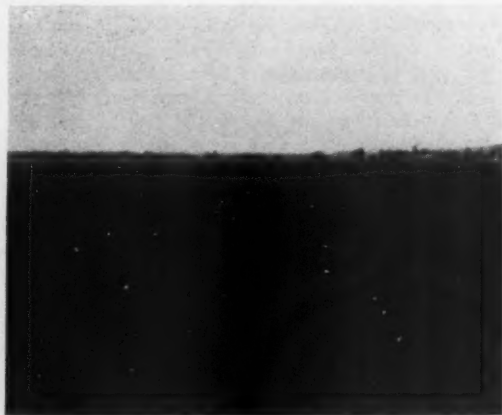


FIG. 15. A closely grazed pasture of the *Poa* consocieties type heavily invaded by *Urtica procera*. July 20, 1935.

where *Urtica* may withdraw from areas of *Poa* but these are not fully ascertained.

Several species of *Polygonum* frequently develop families or colonies on the sites of temporary ponds in the *Poa-Agrostis* grazed communities. *Polygonum punctatum* is the most common species of this group. *Polygonum hydropiper*, *P. persicaria*, and *P. lapathifolium* appear frequently, *P. sagittatum* appears less commonly, and other species are of minor importance.

The *Poa-Agrostis* associates and *Poa* consocieties are invaded by either the *Salix* consocieties or *Salix-Cornus* associates, unless means are taken to prevent this. Several species of *Salix* are aggressive invaders in these grazed areas, much more so than *Cornus stolonifera*. Indeed, the succession sometimes passes from the

TABLE 10. Composition and Frequency of Species in a *Poa* Consocieties Pasture Heavily Invaded with *Urtica procera*, near Madison, July 18, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Poa pratensis</i>	24	96	A
<i>Urtica procera</i>	24	96	616
<i>Aster</i> spp.....	14	56	97
<i>Cirsium arvense</i>	10	40	39
<i>Potentilla norvegica hirsuta</i>	10	40	17
<i>Solidago canadensis</i>	8	32	40
<i>Poa palustris</i>	6	24	1
<i>Erysimum cheiranthoides</i>	4	16	13
<i>Geum strictum</i>	3	12	9
<i>Polygonum convolvulus</i>	3	12	8
<i>Hordeum jubatum</i>	3	12	1
Sedges and rushes.....	3	12	1
<i>Polygonum lapathifolium</i>	2	8	12
<i>Calamagrostis canadensis</i>	2	8	1
<i>Phleum pratense</i>	2	8	1
<i>Stachys palustris</i>	1	4	9
<i>Acrida tuberculata</i>	1	4	9
<i>Leptilon canadense</i>	1	4	2
<i>Erigeron annuus</i>	1	4	1
<i>Rumex acetosella</i>	1	4	1
<i>Rumex crispus</i>	1	4	1
<i>Rorippa hirsuta glabrata</i>	1	4	1
<i>Agropyron repens</i>	1	4	1

Salix consocieties directly to the *Populus-Salix* associates, omitting the *Salix-Cornus* associates.

The composition and frequency of shrubs in an artificially-drained *Poa-Agrostis* pasture are presented in Table 11. Drainage has enabled plants of the

TABLE 11. Composition and Frequency of Woody Species in a *Poa-Agrostis* Associates Pasture, near Deerfield, July 13, 1935.

	Number of quadrats in which each species was found ¹		Total number of individual plants
	Total	Percent	
<i>Salix petiolaris</i> ²	22	88	31
<i>Spiraea alba</i> ³	10	40	14
<i>Betula pumila glandulifera</i> ⁴	2	8	2
<i>Ribes hirtellum</i>	1	4	1

¹Size of each quadrat was nine square meters.

²Very bushy plants 2 to 5 feet tall.

³Low shrubs 1 to 3 feet tall.

⁴Very bushy plants 4 to 6 feet tall.

Poa-Agrostis associates stage to invade and replace a *Calamagrostis-Carex* community. *Salix petiolaris*, a shrubby willow, may have become established during either one of the stages. Many of the *Salix* plants are large and very bushy indicating that they have been present for many years.

In conclusion, it may be stated that drainage, cutting and grubbing of trees and shrubs, mowing, and grazing exert individual and interrelated influences in determining the types of subseres (Figs. 4 and 7).

SUBSERES ON BURNED LANDS

Burning is a practice often intentionally utilized to remove unsightly vegetation and with slight success to control the composition of the vegetation. The use of fire for driving game from the marshes, the spreading of sparks by locomotives, and in fact, any burning likely to ignite the peat are to be condemned.

Most of the burning is done during the late winter and early spring when the vegetation is dry. The effects produced upon the peat soils and upon the native vegetation depend principally upon two factors: (1) whether the soil is frozen, and (2) the amount of moisture in the surface soil.

If the soils are either frozen or wet, burning has little direct effect upon herbs, but usually kills or injures woody vegetation. This explains why burning is commonly practiced on undrained lands when pasturage or hay is desired. Annual mowing is equally effective in preventing the invasion of woody vegetation, but it is much more laborious. If mowing is discontinued for one or more years, burning is necessary to remove debris and destroy shrubs before hay can again be harvested.

The burning of vegetation on peat lands, when the soil is sufficiently dry to ignite, is likely to be detrimental regardless of the depth of the soil burned. Burning of peat on wet lands during dry seasons is usually confined to the upper 1 or 2 inches of soil, but on well-drained lands, the depth of the burn may vary from an inch to several feet.

Three degrees of burning may be distinguished: (1) superficial burning, in which a little of the surface peat is burned and only a part of the vegetation cover is usually destroyed; (2) medium burning, in which the peat is burned to a considerable depth, several inches to several feet, but a layer of peat still remains and all or nearly all of the vegetation is destroyed; (3) deep burning, in which the peat is burned down to the underlying substratum of either mineral soil, sand, or marl and the vegetation is completely destroyed.

Superficial Burning

Annual or occasional shallow burning causes a differential response by the many species of herbaceous vegetation. Certain species such as *Poa pratensis*, *Agrostis alba*, *Calamagrostis canadensis*, *C. inexpectata*, several other grasses, the sedges and the rushes are severely damaged by shallow burning of the peat. Most of the forbs, particularly the weedy ones, and

a few grasses such as *Spartina pectinata* and *Muhlenbergia foliosa* are better adapted to withstand superficial burning. The damage to this latter group is usually more than compensated for by the release of the plants from competition.

Table 12 contains data on the composition of an artificially-drained Calamagrostis-Carex hay meadow, which had been heavily invaded by weedy forbs following frequent superficial burning. *Calamagrostis canadensis* and the sedge and rush group had been damaged to such an extent that they appeared only

TABLE 12. Composition and Frequency of Species in a Drained Calamagrostis-Carex Associates Meadow Heavily Invaded by Forbs as a Result of Frequent, Superficial Burning, near Madison, August 7, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Solidago</i> spp.	25	100	888
Sedges and rushes . . .	24	96	F
<i>Muhlenbergia foliosa</i> . . .	24	96	I
<i>Calamagrostis canadensis</i> . . .	22	88	F
<i>Viola</i> spp.	21	84	149
<i>Cirsium muticum</i> . . .	18	72	40
<i>Dryopteris thelypteris</i> . . .	17	68	357
<i>Lycopus uniflorus</i> . . .	14	56	36
<i>Thalictrum dasycarpum</i> . . .	13	52	171
<i>Lycopus americanus</i> . . .	12	48	31
<i>Aster</i> spp. ¹ . . .	10	40	177
<i>Eupatorium maculatum</i> . . .	9	36	29
<i>Asclepias incarnata</i> . . .	7	28	14
<i>Salix petiolaris</i> . . .	6	24	11
<i>Salix discolor</i> . . .	6	24	9
<i>Helianthus giganteus</i> . . .	5	20	66
<i>Steironema quadriflorum</i> . . .	5	20	25
<i>Salix candida</i> . . .	5	20	10
<i>Gentiana andrewsii</i> . . .	4	16	6
<i>Aster puniceus</i> . . .	3	12	19
<i>Ambrosia artemisiifolia</i> . . .	3	12	11
<i>Fragaria virginiana</i> . . .	2	8	17
<i>Potentilla norvegica hirsuta</i> . . .	2	8	15
<i>Iris virginica</i> . . .	2	8	15
<i>Scutellaria epilobifolia</i> . . .	2	8	2
<i>Lythrum alatum</i> . . .	2	8	2
<i>Apocynum cannabinum</i> . . .	1	4	3
<i>Taraxacum officinale</i> . . .	1	4	2
<i>Betula pumila glandulifera</i> . . .	1	4	2
<i>Salix bebbiana</i> . . .	1	4	1
<i>Hypericum virginicum</i> . . .	1	4	1
<i>Sium suave</i> . . .	1	4	1
<i>Salix pedicularis</i> . . .	1	4	1
Unidentified forb . . .	1	4	1

¹Except *Aster puniceus*.

as "frequent" in 22 and 24 of the quadrats, respectively, instead of as "abundant" in each of the 25 quadrats as would normally have been true had burning not occurred. Drainage alone could account for the reduced abundance of these species, but if the reduction had been due only to drainage, other species such as *Poa pratensis*, *Agrostis alba*, and *Andropogon furcatus* representing a new stage of succession would probably have invaded the area.

The group of plants that invades and replaces the Calamagrostis-Carex vegetation under this treatment is a weedy forb stage recognized as the Solidago-Aster associates (Fig. 16). Plants of *Solidago* spp. appeared in each of the 25 quadrats with an average

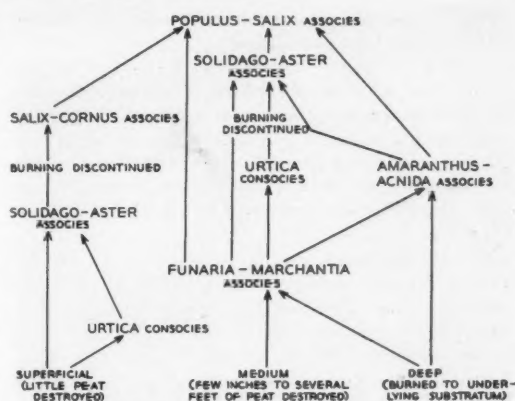


Fig. 16. Effect of burning upon plant successions.

of 36 plants per quadrat (Table 12). Plants of *Aster* spp. appeared in 10 quadrats with an average of 7 plants. There was also a wide assortment of forbs, representing both reliets of the disappearing Calamagrostis-Carex associates and pioneers of the developing Solidago-Aster associates.

Muhlenbergia foliosa appeared in 96 percent of the quadrats and had increased with the incoming stage of succession. Although it does not appear that the plants of this species would be well adapted to withstand burning, this perennial grass frequently invades and persists in those areas where annual or occasional superficial burning is practiced. *M. foliosa* can take advantage of reduced competition because it seeds abundantly the first season.

There were scattered plants of 5 species of *Salix* which had become established since the last burning two years previously (Table 12). Occasionally plants of *Betula pumila glandulifera* and of *Cornus stolonifera* appear in such an environment making it apparent that if burning were discontinued the Solidago-Aster associates would be replaced by the Salix-Cornus type.

The Solidago-Aster associates consists principally of weedy forbs (Fig. 17). The more characteristic species are *Solidago* spp., *Aster* spp., *Eupatorium* spp., *Urtica procera*, *Muhlenbergia foliosa*, *Helianthus giganteus*, *Thalictrum dasycarpum*, *Ambrosia artemisiifolia*, *Viola* spp., and *Polygonum* spp. The species of Solidago and Aster which reproduce aggressively by underground vegetative organs are especially common. *Solidago canadensis* and *S. serotina* are the two most common species.

For reasons previously noted, *Urtica procera* is especially aggressive upon the superficially-burned peat lands (Fig. 18). It usually appears abundantly in local areas. An example of its having invaded shallowly-burned peat land is reported in Table 13. *Urtica* dominated this community so completely that there were only 5 other species represented in small numbers in the 25 quadrats. There was an average of 86 *Urtica* plants per quadrat.

It has not been determined how successfully *Urtica* can compete with other characteristic species of the



FIG. 17. An artificially-drained, superficially-burned area occupied by the *Solidago-Aster* associates. July 20, 1935.

TABLE 13. Composition and Frequency of Species in an *Urtica* Consociates Area, near Deerfield, July 8, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Urtica procera</i>	25	100	2159
<i>Polygonum convolvulus</i>	3	12	5
<i>Sambucus canadensis</i>	1	4	6
<i>Eupatorium maculatum</i>	1	4	2
<i>Muhlenbergia foliosa</i>	1	4	8
<i>Phragmites communis</i>	1	4	1



FIG. 18. A plant community of *Urtica procera* on artificially-drained land which has been superficially burned repeatedly. March 23, 1935.

Solidago-Aster associates. However, since *Urtica* can dominate an area so completely it is recognized as an *Urtica* consociates of this associates. It is probably replaced gradually by species of *Solidago* and *Aster*, particularly if burning is discontinued. In the latter instance, this may occur before the vegetation is finally taken over by the *Salix-Cornus* associates.

The superficial burning of peat soils has been the most common type and has produced undesirable

types of vegetation on thousands of acres of peat land in Dane County.

Medium Burning

This type of burning peat has occurred less frequently but is much more destructive than the superficial type (Figs. 19 and 20). It has not occurred so commonly in Dane County but it has destroyed thousands of acres of peat lands in other parts of the state. In this county the peat beds are smaller.



FIG. 19. A peat bed burned to a depth of several inches during 1934. March 23, 1935.

more extensively cultivated and, hence, less often burned. There is also a more concentrated human population so that greater efforts are taken to prevent and control fires.

In medium burning, the depth of the peat burned varies from several inches to about four feet. The peat may burn to a rather uniform depth, destroying all of the cover, or unburned islands of peat may be left, usually covered with vegetation. A layer of ashes remains, varying from less than one inch to about 12 inches in depth. In some instances, the



FIG. 20. Ditch bank of peat destroyed by fire during 1934. March 23, 1935.

ashes are moved by wind or water erosion, thereby piling up in some places and leaving exposed raw peat in other places.

Since burning of this type is so severe that the vegetation is destroyed, pioneer species appear on the completely denuded land. It is possible that seeds of certain species could be embedded in the lower strata of the peat soils, be exposed upon the burning of the upper layer of the peat, and subsequently germinate. However, the kind of vegetation which

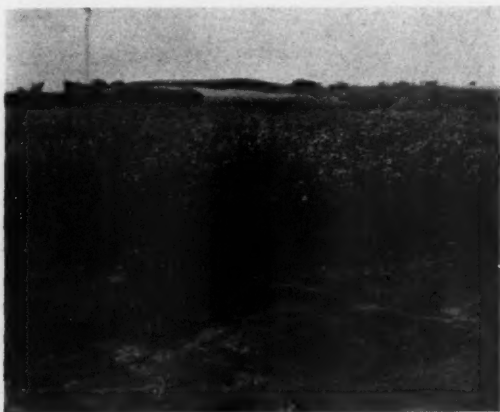


FIG. 21. *Cirsium arvense* growing from underground parts which were sufficiently embedded so that they escaped destruction when fire destroyed a layer of peat during 1934. July 20, 1935.

appears upon the denuded lands largely precludes this possibility. Occasionally, certain species with deep, underground, propagative organs escape destruction. For example, *Cirsium arvense* has been noted to survive and grow luxuriantly upon moderately burned peat land where all other vegetation had been killed (Fig. 21).

The kind of vegetation and the rapidity with which it will appear on these denuded lands depend to a considerable extent upon the moisture relations. The burned-over areas seldom remain barren for a period of more than a few months (Fig. 22). As soon as the ashes become thoroughly moistened and packed, an environment is created upon which certain species can grow. If the burning occurs during the spring or early summer months, vegetation may appear during the latter part of the same season.

The burned-over lands are heavily sown with spores of the bryophytes which usually appear as the pioneer species. *Funaria hygrometrica* is an especially common moss; *Marchantia polymorpha* appears abundantly in the wetter habitats; *Bryum argenteum* and *Ceratodon purpureus* are also quite commonly present. The *Funaria*-*Marchantia* associates frequently appears as a beautiful green carpet over the ashes. In dry periods, the plants are generally confined to depressions and shaded areas. *Funaria*, *Bryum*, and *Ceratodon*, although requiring periodical humidity, are fairly xeric, and are generally distributed over these burned areas. *Marchantia* is decidedly hydro-

phytic and is confined to the moist areas. Spermatophytes are handicapped as pioneers by the lower mobility of their propagules and by lower tolerance to the highly concentrated soil solutions. It is only in the dry situations that some of the flowering plants appear first, and through their reaction on the light factor, permit establishment of an understory of bryophytes.

The second group of invaders on the burned-over lands is either the *Populus*-*Salix* associates, the *Solidago*-*Aster* associates or one of its subdivisions, the *Urtica* associates, or the *Amaranthus*-*Acnida* associates (Fig. 16). The last named is the annual weed stage. Instances were noted where each of these four stages appeared as the pioneer unit of vegetation on recently-denuded areas, but they are usually the second stage of the subseres. The kind of species and consequently the stage of succession, that appear, depend for the most part upon the proximity of parent plants to the burned-over lands and the mobility of their propagules. The dominant species of these four communities are quite generally distributed over the county and, therefore, any or all of them readily act as pioneers.

The data in Tables 14, 15, and 16 were obtained from three typical medium burns. The bryophytic species, *Funaria hygrometrica* and *Marchantia polymorpha*, appear in all three areas; *F. hygrometrica* being abundant in all areas. *Bryum argenteum* and *Ceratodon purpureus* were observed as well as other species less abundant and difficult to identify.



FIG. 22. A peat bed burned to a depth of several inches during 1934. Note the scarcity of vegetation. July 20, 1935.

The vegetation of the first area was growing in a rather dry environment. The peat had been burned to an average depth of approximately 1 foot during the summer of 1934. On June 15, 1935, the area was still quite barren of vegetation except for a thin, discontinuous carpet of *Funaria*, scattered families of *Marchantia*, and a few *Urtica* seedlings. On July 3, the seedlings of a number of weedy forbs had appeared. The composition studies were taken on July 25. On this date, in addition to the bryophytes,

TABLE 14. Composition and Frequency of Species on a Peat Area Moderately Burned During 1934, near Madison, July 25, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Funaria hygrometrica</i> ¹	25	100	A
<i>Marchantia polymorpha</i> ¹	1	4	S
<i>Panicum capillare</i>	18	72	42
<i>Salix</i> spp.....	19	76	49
<i>Muhlenbergia foliosa</i>	12	48	20
<i>Urtica procera</i>	10	40	19
<i>Populus tremuloides</i>	9	36	15
<i>Roripa hispida glabrata</i>	6	24	6
<i>Eupatorium maculatum</i>	3	12	6
<i>Amaranthus gracilians</i>	2	8	3
<i>Taraxacum officinale</i>	1	4	2
<i>Solidago</i> sp.....	1	4	1
Unidentified forb.....	1	4	1
Unidentified forb.....	1	4	1

¹There were other species of bryophytes present but these were less abundant and difficult to identify accurately.

plants of *Panicum capillare*, *Muhlenbergia foliosa*, *Urtica procera*, *Populus tremuloides*, and *Salix* spp. were abundant (Table 14).

The environment of the second burned-over area was considerably wetter than that of the first. Bryophytes appeared in the fall of 1934 following the summer during which the burn occurred. On June 1, 1935, these simple plants, with a few weed seedlings, formed a thin, green carpet over the layer of ashes. One month later a heavy green carpet of abundantly

TABLE 15. Composition and Frequency of Species on a Peat Area Moderately Burned During 1934, near Middleton, July 24, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Funaria hygrometrica</i> ¹	25	100	A
<i>Marchantia polymorpha</i> ¹	22	88	F
<i>Populus tremuloides</i>	25	100	157
<i>Solidago</i> spp.....	24	96	95
<i>Leptilon canadense</i>	21	84	43
<i>Erechtites hieracifolia</i>	14	56	10
<i>Erigeron annuus</i>	11	44	18
<i>Apocynum androsaemifolium</i>	10	40	11
<i>Muhlenbergia foliosa</i>	8	32	8
<i>Cirsium lanceolatum</i>	7	28	7
<i>Salix</i> spp.....	6	24	14
<i>Lycopus americanus</i>	6	24	6
<i>Typha latifolia</i>	4	16	4
<i>Solanum nigrum</i>	4	16	4
<i>Potentilla norvegica hirsuta</i>	4	16	4
<i>Cyperus strigosus</i>	3	12	5
<i>Taraxacum officinale</i>	3	12	3
<i>Populus deltoides</i>	2	8	2
<i>Lactuca scariola integrata</i>	2	8	2
<i>Epilobium angustifolium</i>	1	4	1
<i>Erigeron ramosus</i>	1	4	1
<i>Digitaria sanguinalis</i>	1	4	1
<i>Polygonum lapathifolium</i>	1	4	1
<i>Chenopodium album</i>	1	4	1
<i>Urtica procera</i>	1	4	1
<i>Pilea pumila</i>	1	4	1
<i>Lactuca spicata</i>	1	4	1

¹There were other species of bryophytes present but these were less abundant and difficult to identify accurately.

fruiting bryophytes had developed, and seedlings of weedy forbs were numerous. Seedlings of *Populus tremuloides* and *Salix* spp. had appeared. The data presented in Table 15 were obtained on July 24. *Populus tremuloides*, *Salix* spp., *Solidago* spp., *Leptilon canadense*, *Erechtites hieracifolia*, *Erigeron annuus*, *Apocynum androsaemifolium*, and *Muhlenbergia foliosa* had appeared in considerable numbers, and a number of other species were less abundant.

The rapid growth of woody species here is indicated by the following average height measurements of 10 of the oldest-appearing plants on August 16, 1935: *Populus tremuloides*, 32 inches; *P. deltoides*, 13 inches, and *Salix* spp., 17 inches.

TABLE 16. Composition and Frequency of Species on a Peat Area Moderately Burned During 1934, near Madison, August 7, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Populus deltoides</i>	25	100	175
<i>Populus tremuloides</i>	19	76	37
<i>Salix</i> spp.....	25	100	407
<i>Funaria hygrometrica</i> ¹	25	100	A
<i>Marchantia polymorpha</i> ¹	15	60	S
<i>Typha latifolia</i>	24	96	173
<i>Solidago</i> spp.....	18	72	90
<i>Taraxacum officinale</i>	5	20	6
<i>Erechtites hieracifolia</i>	3	12	6
<i>Aster puniceus</i>	2	8	3
<i>Muhlenbergia foliosa</i>	2	8	3
<i>Panicum capillare</i>	2	8	2
<i>Euphorbia maculata</i>	1	4	1
<i>Epilobium coloratum</i>	1	4	1
<i>Leptilon canadense</i>	1	4	1
<i>Eupatorium maculatum</i>	1	4	1
<i>Cirsium muticum</i>	1	4	1
<i>Solanum nigrum</i>	1	4	1
<i>Polygonum lapathifolium</i>	1	4	1
Unidentified forb.....	1	4	1

¹There were other species of bryophytes present but these were less abundant and difficult to identify accurately.

The third tract was a small, moderately burned, peat area near a drainage ditch, along which were growing a number of *Populus deltoides* and *Salix* plants, while the nearest *Populus tremuloides* was one-fourth mile distant. Accordingly, seedlings of *P. tremuloides* were less abundant on the burned area than those of *P. deltoides* and *Salix*. Since *Typha latifolia* was growing in the drainage ditch, seedlings of it appeared on the burned-over land. *Solidago* spp. appeared abundantly in 18 of the 25 quadrats (Table 16).

From an analysis of Tables 14, 15, and 16 and from numerous observations made on other moderately-burned areas, it is apparent that many phanerogams invade these areas shortly after the appearance of the initial bryophytic stage. Certain species are capable of invading rapidly because (1) they seed abundantly and the seeds are broadly disseminated, and (2) the plants become readily adapted to the environment of the burned-over land. *Populus tremuloides*, *P. deltoides*, and several species of *Salix* are the common, woody species. The more common,

early-invading, herbaceous species are *Urtica procera*, *Solidago* spp., *Aster* spp., *Leptilon canadense*, *Erechtites hieracifolia*, *Erigeron annuus*, *Typha latifolia*, *Acnida tuberculata*, *Chenopodium album*, *Amaranthus* spp., *Muhlenbergia foliosa*, *Panicum capillare*, *Sisymbrium altissimum*, and *Rorippa hispida glabrata*.

In midsummer, 1935, data were obtained relative to the woody species of an area moderately-burned during 1932 (Table 17). The *Populus-Salix* associes is the prevailing type of vegetation with *Populus tremuloides* and six species of *Salix* appearing abun-

TABLE 17. Composition and Frequency of Woody Species on an Area Severely Burned During 1932, near Marshall, July 11, 1935.

	Number of quadrats in which each species was found ¹		Total number of individual plants
	Total	Percent	
<i>Populus tremuloides</i>	18	72	50
<i>Salix nigra</i>	25	100	338
<i>Salix cordata</i>	25	100	154
<i>Salix petiolaris</i>	9	36	19
<i>Salix lucida</i>	9	36	13
<i>Salix longifolia</i>	8	32	12
<i>Salix discolor eriocephala</i>	6	24	10

¹The size of each quadrat was nine square meters.

dantly. Several herbaceous species were also well represented. The average height of 10 of the larger *Populus tremuloides* on another peat area burned during the summer of 1932 was 129 inches on August 26, 1935. This is an indication of how well this species flourishes on such an environment.

The subseres on those lands where burning has completely destroyed the cover and removed much but not all of the peat may be summarized as follows: The pioneer stage is the *Funaria-Marchantia* associes followed by either the *Solidago-Aster* associes (or one of its subgroups, the *Urtica* consocies), the *Populus-Salix* associes, or the *Amaranthus-Acnida* associes (Fig. 16). Any of the stages are subsequently replaced either directly or indirectly by the *Populus-Salix* associes if burning is discontinued. The *Populus-Salix* associes is recognized as subclimax on these burned-over lands.

A number of observations were made where moderately burned land was under cultivation. The success of the crops depends principally upon three factors, namely, (1) depth of burn, (2) preparation of seedbed, and (3) water relations. If the layer of ashes is shallow, it can be readily incorporated into the underlying peat and crops can usually be grown successfully. If the layer of ashes is deep, it is much more difficult to work the ash layer into the underlying peat. Crops grow poorly on the pure ash layer. Accordingly, any methods of seedbed preparation which mix the ashes with the underlying peat are of much value. Burning may lower the soil surface so that it is too close to the water table for successful cropping.

Deep Burning

Lastly, there is that type of burning whereby the entire depth of the peat is destroyed down to the

underlying substratum. The species that invade land from which all the peat is burned are similar to those that appear on the moderately-burned areas where an underlying peat layer remains. One major difference is that the environment created by the former type is less favorable to the vegetation than that created by the latter. The result is that land, where the entire depth of peat has been destroyed, remains bare longer. The vegetation which finally invades this environment is usually not thrifty and shows clearly the characteristic effects of nitrogen deficiency. The ash layer also has a high concentration of soil solutes, which is probably detrimental to vegetation.

The *Funaria-Marchantia* associes is usually the pioneer community and this is followed by any one of the four types of vegetation which follow the pioneer stage in those areas where the entire peat layer is not destroyed.

There is one difference, however, in that the annual weedy-forb, *Amaranthus-Acnida* associes, plays a more important role (Fig. 16). Since the soil remains barren for considerable time, this seral stage sometimes becomes the pioneer unit or at least it is frequently interpolated in the early stages of succession. It is especially likely to appear on those burned-over lands which are near cultivated lands. The more common species of this associes are *Amaranthus hybridus*, *A. retroflexus*, *A. graecizans*, *Acnida tuberculata*, *Chenopodium album*, *Sisymbrium altissimum*, *Panicum capillare*, and *Erigeron annuus*.

Peat lands supporting desirable native vegetation are commonly rendered worthless for cultivation and other economic usage by this deep burning. It represents the most serious type of destruction. However, such land may eventually produce a satisfactory stand of usable timber of the dominant species of the *Populus-Salix* associes.

SUBSERES INDUCED BY SOIL DISTURBANCES

Soil disturbances associated with the digging of drainage ditches, the consequent formation of ditch banks, the tramping by livestock, and the removal of peat for fuel are of much less importance than those previously discussed.

There are many miles of ditches in Dane County as a result of the artificial-drainage projects. The ditches may conduct water continuously or intermittently, depending principally upon their size and depth and upon the extent of the drainage area. In some instances, natural water courses have been deepened and widened to improve drainage.

The vegetation in these ditches is usually of the hydrophytic type. Common species are: several species of sedges and rushes, *Alisma plantago-aquatica*, *Equisetum fluviale*, *Impatiens biflora*, *Mentha arvensis canadensis*, *Polygonum* spp., *Sagittaria latifolia*, *Sium suave*, *Cicuta bulbifera*, *Lycopus uniflorus*, *Mimulus ringens*, *Radicula nasturtium-aquaticum*, *Penthorum sedoides*, *Prunella vulgaris*, *Typha latifolia*, *Glyceria striata*, and *Agrostis alba*.

The bare ditch banks are usually invaded first by weedy forbs. The subsequent types of vegetation de-

pend upon the kind of treatment and kind of vegetation on adjoining lands. Seedlings of *Populus* and *Salix* frequently appear on these banks with or after invasion by the weedy-forb stage. Many miles of ditch banks are covered with dense stands of *Salix* alone or mixed with *Populus tremuloides*, or *P. deltoides*, or both (Fig. 23). Some ditch banks have



FIG. 23. A dense stand of *Salix* spp. growing along a ditch bank. July 20, 1935.

been invaded by the same type of vegetation that prevails on adjoining lands. For example, ditch banks located in pasture lands occupied by the *Poa-Agrostis* associates are frequently covered by that type and the smaller ditch banks located on land covered with *Calamagrostis-Carex* associates vegetation are invaded by that type.

In addition, two other types play an important role in the vegetation of ditch banks. These are the *Urtica* consociates previously discussed, and the *Ambrosia* consociates of the *Amaranthus-Aenida* associates. *Urtica procera* frequently invades these banks and eventually occupies extensive tracts, commonly dominating the ground to the nearly complete exclusion of other species (Fig. 24). *Ambrosia trifida* also



FIG. 24. *Urtica procera* growing along a drainage ditch. July 20, 1935.



FIG. 25. *Ambrosia trifida* growing on a ditch bank. July 20, 1935.

thrives especially well on these fertile, usually alkaline soils along the ditches. This species seeds abundantly; the seedlings grow rapidly, and because they are usually present in dense, tall stands, invasion is often complete (Figs. 25 and 26). There were 2,115 plants of *Ambrosia* on the 25 quadrats in one of these ditch-bank communities (Table 18). *Urtica* was increasing and will probably eventually replace *Ambrosia* as the major dominant.

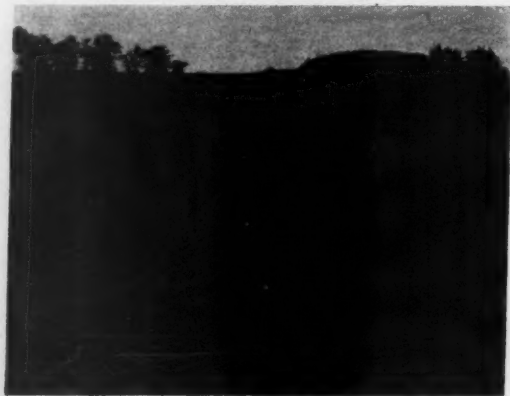


FIG. 26. An *Ambrosia trifida* community which failed to perpetuate itself. July 20, 1935.

In addition to grazing, heavy tramping by livestock greatly affects the vegetation in local areas around watering tanks, ponds, and gates where animals usually destroy much or all of the vegetation. The soil either remains bare or is covered by the weedy-forb stage which is maintained as long as heavy tramping continues.

Only one example was found of the removal of peat bricks for fuel. Six feet of peat were removed to

TABLE 18. Composition and Frequency of Species in an Ambrosia Consocieties on a Ditch Bank, near Deerfield, July 7, 1935.

	Number of quadrats in which each species was found		Total number of individual plants
	Total	Percent	
<i>Ambrosia trifida</i>	25	100	2115
<i>Urtica procera</i>	3	12	7
<i>Urtica procera</i> (seedlings).....	21	84	249
<i>Erysimum cheiranthoides</i>	21	84	162
<i>Pilea pumila</i>	17	68	167
<i>Chenopodium album</i>	15	60	169
<i>Capella bursa-pastoris</i>	9	36	71
<i>Bidens vulgata</i>	8	32	11
<i>Galium aparine</i>	6	24	120
<i>Elymus virginicus</i>	5	20	13
<i>Acrida tuberculata</i>	4	16	5
<i>Poa palustris</i>	4	16	5
<i>Sisymbrium altissimum</i>	3	12	6
<i>Parietaria pennsylvanica</i>	3	12	5
<i>Impatiens biflora</i>	3	12	3
<i>Cyperus strigosus</i>	2	8	3
<i>Veronica peregrina</i>	2	8	3
<i>Leptilon canadense</i>	2	8	2
<i>Erigeron annuus</i>	2	8	2
<i>Melilotus alba</i>	2	8	2
<i>Polygonum</i> sp.....	2	8	2
<i>Malva rotundifolia</i>	2	8	2
<i>Potentilla norvegica hirsuta</i>	2	8	2
<i>Acer negundo</i> (seedlings).....	1	4	2
<i>Trifolium repens</i>	1	4	2
<i>Cirsium muticum</i>	1	4	1
<i>Poa compressa</i>	1	4	1

the water table. No vegetation had appeared on the small barren area, two years hence.

SUMMARY

Ecological studies of the vegetation were conducted on the peat lands of Dane County, Wisconsin, particularly with respect to the nature of the plant successions. The secondary plant successions, brought about by a number of introduced, biotically-controlled factors, namely, artificial drainage, cutting and grubbing of trees and shrubs, mowing, grazing, burning, and concomitant soil disturbances are emphasized.

Peat lands comprise 52,288 acres or 6.8 percent of the total county area, nearly all located within the glaciated part of the county. The peat, chiefly of the water-deposited type, occurs in numerous beds of various sizes.

The natural drainage systems of the peat lands are in an immature stage of development. Between 1900 and 1926, approximately 40 per cent of the peat land was artificially drained by 18 major projects.

The existing evidence is that the vegetation of much of the peat land at the time of settlement consisted of two principal types, the *Larix* consocieties and the *Calamagrostis-Carex* associates. The *Larix* consocieties are quasi-stable and accordingly recognized as preclimax.

The two primary plant successions which have been of importance on the peat lands are the bog sere and the hydrosere. The bog sere was the most common type in the past, but has largely disappeared. Only relicts were found of a number of the developmental

stages. The *Larix* consocieties has been the most tolerant of the changing environmental conditions and it still occupies a small acreage of peat land. The primary plant succession is, at present, almost entirely of the hydrosere type because of more effective drainage. The *Populus-Salix* associates is recognized as subclimax to the *Quereus-Carya* association although conclusive evidence is lacking as to the true climax.

Introduced biotically-controlled disturbance has been so general that much of the vegetation on the peat lands is now undergoing secondary succession. These successions are discussed and traced from the *Larix* consocieties and the *Calamagrostis-Carex* associates stage of vegetation in relation to the factors of artificial drainage, cutting of trees, mowing, and grazing. Specific suggestions are made as to the most economically-desirable ecological treatment of the various vegetational stages.

The burning of the vegetation on wet or frozen peat has little effect on herbaceous vegetation but will usually prevent the ecesis of shrub and tree species. If the peat is dry, burning frequently results in various degrees of destruction of both peat and vegetation. Three degrees of burning are recognized, namely, superficial, medium, and deep. The subseres following burning are discussed.

Other peat disturbances, the most important of which are the digging of drainage ditches and the consequent formation of ditch banks, play a role in modifying the vegetation.

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